Swan-plant interactions in a chalk river catchment

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Abstract

"Swan-plant interactions in a chalk river catchment". Kevin A. Wood

Plants are of fundamental importance to the structure, functioning and service provision of many ecosystems. However, herbivores can have negative ecological and socioeconomic effects on plant communities through consumption, trampling and alteration of nutrient cycles. In this thesis I address a particular herbivore-plant interaction: the grazing of plants in chalk river catchments, principally the submerged macrophyte water crowfoot (*Ranunculus penicillatus ssp. pseudofluitans* (Syne) S.D. Webster) and terrestrial pasture grass species, by flocks of non-breeding mute swans (*Cygnus olor* Gmelin, 1789). This research was carried out over two years in the River Frome catchment (Dorset, UK).

Based on a meta-analysis of previous waterfowl grazing studies I show that waterfowl biomass density (kg ha^{-1}) rather than individual density (ind. ha^{-1}) is a better predictor of reductions in plant standing crop. Most studies to date have analysed such reductions using only individual densities, despite large between-taxa variation in waterfowl body mass, diet and intake rates. I quantified the abundance, species richness, evenness, flowering and dominance of the chalk river aquatic plant community in relation to biotic and abiotic factors during the growth-, peak-, and recession-phases of the growth cycle. The relative importance of herbivory, riparian shading, water temperature and distance downstream varied between different phases of the plant growth cycle, highlighting the importance of seasonal patterns in regulation of plant community structure.

The River Frome swan population varied seasonally, being highest in the winter. The population was dominated by non-breeding adults and juveniles that lived in flocks. These flocks exhibited strong seasonal habitat switches between terrestrial pasture in winter and spring, and river in summer and autumn. I provided evidence that this switch was linked to the seasonal decrease in water velocity between spring and summer, which reduced the metabolic costs of river feeding and increased the relative profitability of aquatic food resources. I used a mathematical population model and an individual-based behavioural model respectively to explore two management options for the alleviation of the swan grazing conflict in chalk rivers: population control and habitat alterations. Population control measures, such as clutch manipulations, fertility control, culling or translocations, were predicted to be unsuccessful except at impractically high levels of management effort, due to the effects of immigration and high survival rates in offsetting removed eggs or individuals. Habitat alterations, in particular the narrowing of river channels to cause a local increase in water velocity and thus swan foraging costs, are more promising management options as they require lower management effort, are less ethically controversial, and address the fundamental reason why swans select their food resources, the rate of net energy gain ('profitability').

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Despite the generous help and advice which I have received whilst undertaking this work, the fault for any mistakes contained within remains mine and mine alone.

Author's declaration

I confirm that the work presented in this thesis is my own work, with the following exceptions:

Chapter 2 is published in collaboration with Richard Stillman, Ralph Clarke, Francis Daunt and Matthew O'Hare as:

Wood, K.A., Stillman, R.A., Clarke, R.T., Daunt, F. & O'Hare, M.T. (2012) The impact of waterfowl herbivory on plant standing crop: a meta-analysis. *Hydrobiologia*, **686**, 157-167.

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In addition, the individual-based model used in Chapter 8 used the MORPH framework created by Stillman (2008). The data on swan numbers, relative patch use and water crowfoot biomass used in Chapter 8 were those given by O'Hare *et al*. (2007).

Kevin A. Wood (May 2012)

Chapter 1: Swan-plant interactions in a chalk-river catchment: an introduction.

One of the most striking features of our planet is the dominance of plants on its lands and in its waters. Plants help to shape the world around them, and as a consequence the Earth and the ecosystems it contains would be very different without them. This introduction will outline the current understanding of plant-herbivore interactions, with a deliberate focus on waterfowl and aquatic plants reflecting the subject of this thesis. Details of the chosen study system, and its suitability for the study of plant-herbivore investigations, will also be given. This introductory chapter will conclude by setting out the main questions that will be addressed in the rest of this thesis.

1.1 The roles of plants in ecosystems

A common feature of many terrestrial and aquatic ecosystems is the fundamental importance of plants to ecosystem structure, function and service provision (Grime, 2002; Moss, 2010). Plants both provide and diversify the habitat within a ecosystem, which can then be used by other organisms (Hearne & Armitage, 1993; Armitage & Cannan, 2000). For example, plants provide support structures for a range of epiphytic organisms, from algae to insect larvae, to live on (Lampert & Sommer, 2007). Plants with complex architectures (*i.e.* extensive branching) tend to support higher biomasses of organisms per gram of plant compared with simple plants (Cheruvelil *et al*., 2002; McAbendroth *et al*., 2005; but see Cyr & Downing, 1988). Some species of fishes and amphibians use plants as support structures for spawning and cannot reproduce successfully in the absence of plants (Allouche, 2002; Davies *et al*., 2004). Plants can provide refugia for other organisms from predators as well as adverse environmental conditions such as extreme winds, water flows and temperatures (Stansfield *et al*., 1997; Allouche, 2002; Lampert & Sommer, 2007). Invertivorous fish foraging success typically declines with increased plant densities, providing invertebrate prey with refugia (Diehl, 1988). Conversely, some predators use plants for camouflage and as ambush sites (Heck & Crowder, 1991); thus the relationship between plant abundance and predation risk is often specific to the organisms concerned.

Plants have important uses in human civilisation as building materials, medicines and in particular as food. Such uses give plants socioeconomic value and compel their protection from factors that could lead to losses of plant material, such as drought, fire, disease and herbivores. In many developed regions, such as western Europe, agriculture is the dominant land use and has thus shaped the landscape (including waterscape) in which both plants and their herbivores live (Green, 1989; van Eerden *et al*., 1996). In

Britain 18.3 million hectares of land, 75 % of the total, is devoted to agriculture (Robinson & Sutherland, 2002). Intensive agriculture has had profound effects on aquatic ecosystems, in particular through additions of sediment and growth-limiting nutrients (nitrogen and phosphorus), and the abstraction of water (Egertson *et al*., 2004; Lampert & Sommer, 2007; Moss, 2010). Plants are also food for a range of animals in nature (see **Section 1.2**); live plant material is consumed by herbivores whilst dead or decaying plant material is consumed by detritivores (Cebrian & Lartigue, 2004). In aquatic ecosystems such plant material may be the result of autochthonous production, *i.e.* plants within the waterbody, or allochthonous production, *i.e.* riparian plant material transferred into the waterbody (Dawson, 1976b; Lampert & Sommer, 2007).

Within ecosystems plants facilitate the interchange of oxygen and nutrients between different layers of sediment (or soil) and the water column (in aquatic ecosystems) or the atmosphere (in terrestrial ecosystems), as well as exerting an influence on the local light and temperature climate (Landers, 1982; Carpenter & Lodge, 1986; Lampert & Sommer, 2007). For example, the photosynthetic activity of aquatic plants can increase river dissolved oxygen concentrations (Owens & Edwards, 1961). Submerged vascular plants (termed 'macrophytes') can influence river channel geomorphology by increasing frictional resistance to, and diverting, water flow (Clarke, 2002). Macrophytes cause increased sediment deposition within their stands, reducing sediment transport, increasing water clarity and altering substrate characteristics (Wharton *et al*., 2006).

1.2 Herbivore effects on plants: individuals to communities

A wide range of taxa consume living vascular plant tissues (termed 'herbivory'), mainly insects, nematodes, crayfish, gastropods, fish, mammals and birds (Lodge, 1991; Newman, 1991; Lodge *et al*., 1998; Schoonhoven *et al*., 2005). Around 75 % of the extant macroscopic life on Earth, both in terms of biomass and biodiversity, is either a plant or an herbivorous vertebrate, arthropod, mollusc or nematode (Strong *et al*., 1984; Wilson, 2001; Schoonhoven *et al*., 2005; Johnson, 2011).

Herbivores interact with plants by a range of direct and indirect mechanisms. Herbivores remove plant tissues through consumption and non-consumptive destruction, such as trampling and uprooting of plant material that may not be subsequently eaten (Klaassen & Nolet, 2007). Herbivores may also affect plants through consumption and dispersal of propagules, and by altering competitive interactions between plant species. Where

herbivores forage selectively on a species of plant, they may alter competitive interactions and facilitate the competitive release of other plant species and thus alter the absolute and relative abundance of each species (Hidding *et al*., 2010). Herbivores, in particular highly mobile taxa such as birds, are important vectors in the dispersal of plant propagules, transporting seeds and plant fragments between habitats (Clausen *et al*., 2002; Green *et al*., 2002). Such transport can increase connectivity between habitat patches, but can also facilitate the spread of invasive species (Quinn *et al*., 2008). Thus anthropogenic factors such as human disturbance, which alter the densities and behaviours of propagule-transporting animals, can influence patterns of plant establishment within a landscape (Francis *et al*., 2012). The indirect effects of herbivores on plants include alterations to biogeochemical cycles, particularly as the result of faecal deposition (Kitchell *et al*., 1999; Hahn *et al*., 2008). These direct and indirect effects can have a range of effects on plants. Herbivory removes plant tissues, which reduces abundance if the rate of tissue removal exceeds macrophyte growth. Whilst low densities of herbivores may have a negligible or even positive effect on plant abundance, most studies of herbivory by groups of individuals (*i.e.* flocks of birds, herds of ungulates) have reported substantial negative effects of herbivores on plant abundance (Cyr & Pace, 1993; Milchunas & Lauenroth, 1993; Lodge *et al*., 1998). However, these reductions vary in magnitude from 0 to 100 % (Lodge *et al*., 1998). Plant abundance is typically measured as (i) cover (%), the proportion of a given benthic area occupied by macrophytes, (ii) volume occupied (%), the proportion of a given volume of water occupied by macrophytes, and (iii) biomass (g m^{-2}), the mass of plant material in a given area or volume (Murphy, 1990; Gunn *et al*., 2010). Whether these three distinct measures of plant abundance exhibit equivalent responses to herbivory, or even if the three measures are closely related, are not well understood. The densities of shoots, stems and ramets may also be altered by herbivores (Valentine *et al*., 1997; Idestam-Almquist, 1998). A key feature of plant-herbivore interactions is that herbivores graze vegetation but rarely consume all the biomass of an individual plant, and may therefore alter the morphology of grazed plants; O'Hare *et al*. (2007) reported that swan grazing on macrophytes resulted in fewer leaves per stem and a lower stem to leaf ratio. Terrestrial grasses grazed by geese respond by producing more stems per area, resulting in shorter, 'bushier' swards (Best & Arcese, 2009). Short-term reductions in plant abundance associated with herbivores may lead to increased plant growth rates and primary production. Release of the plant from density-limited growth, caused by self-shading or accumulation of senescent material, can allow compensatory growth (McNaughton, 1983; Huntly, 1991; Valentine *et al*., 1997; Nolet, 2004). Such processes may facilitate overcompensation in the growth response and thus increased primary production. Increased primary productivity can facilitate cyclical patterns of grazing and the development of grazing lawns; Prins *et al.* (1980) showed that brent geese (*Branta bernicla* L.) visited the same patches every 3 to 5 days and consumed approximately one-third of the young graminoid

shoots, stimulating both plant species to produce double the biomass of above-ground vegetation relative to ungrazed plants.

Intense herbivory can slow the colonisation of plants, particularly where herbivores forage on belowground tubers (Gunzl, 1993; Parker *et al*., 2006). Herbivores may exhibit a preference for energy-rich, highly digestible flowers and significantly reduce flower abundance (O'Hare *et al.*, 2007; Rodriguez-Villafane *et al.*, 2007). Several studies have demonstrated that herbivory may directly and indirectly alter flowering in grazed plants which then impacts sexual reproduction (Rodríguez-Villafañe *et al*., 2007; Barber *et al*., 2011; Brys *et al*., 2011). The effect of herbivory on patterns of spatial heterogeneity of plant communities is complex, with both increases and decreases reported (Huntly, 1991; Adler *et al*., 2001). Where herbivores forage selectively on a species of plant, or plants do not have equal tolerances to herbivory, foraging can alter competitive interactions between plant species leading to the competitive release of other plant species and thus changes in abundance and distribution (Huntly, 1991; Santamaria, 2002; Sandsten & Klaassen, 2008). Selective herbivory by Eurasian coots (*Fulica atra* L.) altered macrophyte species composition in Lake Zwemlust, the Netherlands, from dominance of *Elodea nuttallii* to *Ceratophyllum demersum* to *Potamogeton berchtholdii* within five years (van Donk & Gulati, 1995). Thus herbivores can be important determinants of plant community properties, such as species richness and evenness, within a habitat (Huntly, 1991).

Removal of plant tissues by herbivores can lead to feedback effects that further affect plants in both positive and negative ways. Bodelier *et al*. (2006) found that swan foraging for macrophyte tubers in a shallow wetland decreased sediment microbial activity, which resulted in greater growth and biomass of the tubers that survived herbivory. Iacobelli & Jefferies (1991) demonstrated that goose grazing reduced vegetation which increased salinity in the exposed soils and caused the death of adjacent ungrazed *Salix* stands, increasing overall herbivore impact on the plant community. Additionally, reduced plant cover caused by intensive geese foraging in salt marsh habitats has been shown to reduce nitrogen availability in soils (Buckeridge & Jefferies, 2007). However, this may be offset by faecal deposition, which can increase nutrient availability to plants and thus increase standing crop (Bazely & Jefferies, 1985).

Most studies of herbivory focus on short-term changes in plant abundance, yet several studies in shallow lakes have documented the role of herbivores in the long-term productivity of plant assemblages. Waterfowl herbivory has been implicated in the

transition of freshwater lakes from the clearwater, plant-dominated state to the turbid, phytoplankton dominated state, resulting in a dramatic long-term suppression of plant biomass (van Donk & Gulati, 1995; Hansson *et al*., 2010). Mechanisms that might underlie a shift of alternative stable states include removal of macrophytes by grazing and non-consumptive damage, and increased lentic nutrient concentrations from avian faecal inputs. Avian faecal contributions of nitrogen and phosphorus are known to be insignificant in most of the waterbodies studied where waterfowl are largely resident (Mitchell & Perrow, 1998). However, substantial nutrient loading by waterfowl has been documented in some instances, often where large flocks of birds feed in nearby terrestrial fields and use the aquatic habitat as a roost, effectively transferring nutrients from terrestrial vegetation to the aquatic habitat (Olson *et al.*, 2005; Hahn *et al.*, 2008).

Reductions in plant abundance due to herbivory can result in individual- and population-level effects on animals which depend on plants for food, shelter or breeding habitat. Evidence from tidal salt marsh ecosystems demonstrated that invertebrate abundance and species richness were reduced as invertebrate habitat was degraded due to intense grazing by geese (Sherfy & Kirkpatrick, 2003). Dixon (2009) found that invertebrate abundance in an intertidal wetland was on average 35 % lower in areas grazed by black swans (*Cygnus atratus* Latham, 1790) relative to exclosures. Impacts on invertebrates may occur even where the proportional reduction of vegetation is low; Bortolus *et al.* (1998) reported reduced abundance of a polychaete in a brackish lagoon where plant biomass had been reduced by 17 % by mixed-species flocks of waterfowl. Many species of small mammal and ground-nesting birds in Arctic marshes depend upon the graminoid vegetation consumed by geese; a negative correlation between goose grazing damage and the abundance and distribution of small mammals has been documented (Samelius & Alisauskas, 2009). The abundance of lemmings and voles in grazed areas can be an order of magnitude lower than in ungrazed areas. Densities of some ground-nesting bird species have decreased due to reduced vegetative cover as lesser snow geese (*Chen caerulescens* L.) populations increased over a 15 year period (Sammler *et al.*, 2008). Newson *et al*. (2012) found evidence that five out of eleven UK woodland bird species studied showed evidence of population declines in response to herbivory by three species of deer with expanding populations; Reeves' muntjac (*Muntiacus reevesi* Ogilby, 1839), roe deer (*Capreolus capreolus* L.) and fallow deer (*Dama dama* L.). However, not all plant-herbivore interactions have negative consequences for other organisms. In particular, herbivores can be important vectors in the dispersal of invertebrates between habitats; viable invertebrate eggs have been recovered from waterfowl faecal material (Charalambidou & Santamaria, 2005; Green *et al*., 2008).

A number of factors can influence the magnitude of effect that herbivores exert on plants. In general, fast-growing less-defended plants suffer greater herbivore damage than slow-growing well-defended plants (Coley *et al*., 1985; Maron & Crone, 2006). The effects of herbivory on plants are often strongly density-dependent, with reductions in plant abundance positively related to herbivore density (Stewart *et al.*, 2006). However, in an analysis of waterfowl reductions of plant standing crop in freshwaters, Marklund *et al.* (2002) reported that some of the greatest reductions were associated with the highest waterfowl numerical densities, but there was no statistically significant relationship between waterfowl numerical density and plant standing crop reduction. Plants can also suffer relatively high losses in abundance due to herbivory (i) where plants exist at low abundance, and (ii) during the colonisation phase of the plant (Marklund *et al*., 2002). An additional consideration should be whether the herbivores and plants are native to the ecosystem in which their interactions occur; in general native herbivores suppress the spread of exotic plants, whereas exotic herbivores facilitate increased abundance and species richness amongst exotic plants (Parker *et al*., 2006).

1.3 Herbivorous waterfowl

Waterfowl is the term given to ducks, geese and swans (Order: Anseriformes). Previous authors have tended to disregard rails, coots, gallinules and allies (Order: Rallidae; hereafter 'rails') when discussing waterfowl (*e.g.* Baldassarre & Bolen, 2006) due to their distant evolutionary relationship to ducks, geese and swans. However, rails exhibit many broad similarities in diet, foraging behaviour and effects on vegetation with other waterfowl (Marklund *et al.*, 2002). Waterfowl are found on every continent except Antarctica and exhibit a wide range of diets (Hughes & Green, 2005; Baldassarre & Bolen, 2006). Within the guild of herbivorous waterfowl there are six principle feeding groups; Rallidae (rails, coots, gallinules and allies), Anatini (dabbling ducks), Aythyini (diving ducks), Tadornini (sheldgeese, shelducks and allies), Cygnini (swans), and Anserini (geese). Based on the information given in Taylor (1998) and Kear (2005), there are 233 species of waterfowl that consume vegetation, with around three quarters of these represented by ducks and rails (**Figure 1.1**). Within the swans and geese all species consume vegetation, whereas within groups of smaller-bodied waterfowl some species are exclusively carnivorous (22 % for rails and 45 % for diving ducks).

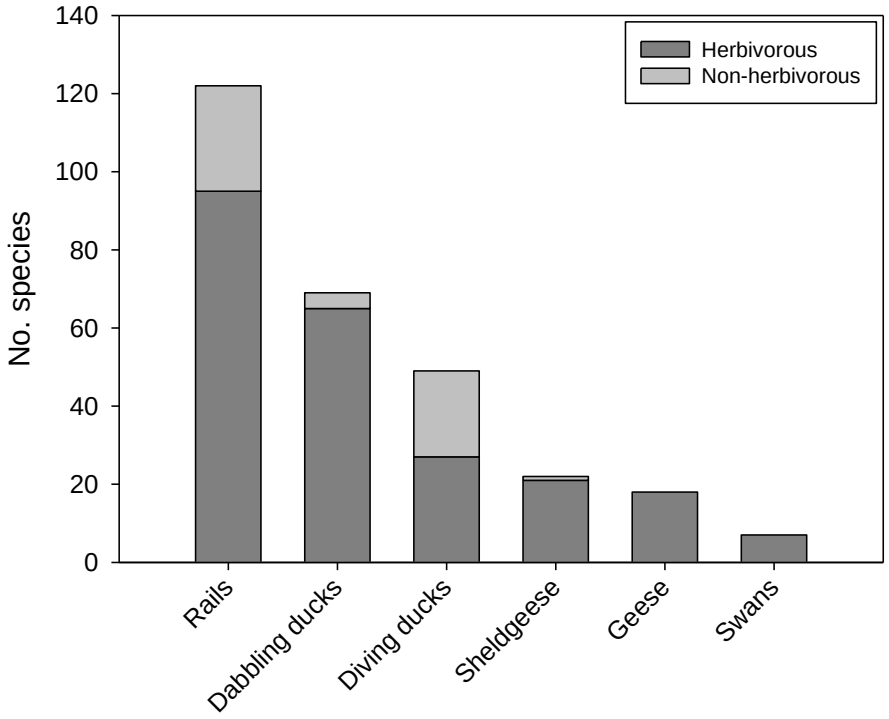


Figure 1.1*: The number of species in each of the six principal groups comprising the waterfowl guild, together with the proportion that consume (dark grey) and do not consume living plant tissues indicated (light grey).*

Herbivorous waterfowl forage on three key plant tissue types: above-ground vegetative tissues such as leaves and stems, below-ground storage tissues such as tubers, and reproductive tissues such as seeds and flowers (Hughes & Green, 2005; Baldassarre & Bolen, 2006). Above-ground vegetative tissues are generally the most accessible in large quantities to waterfowl, relative to below-ground tissues which must be located and unearthed, and reproductive tissues which are only available for a short period of the year. However, both belowground storage tissues and reproductive tissues have higher energy content than above ground vegetative tissues, and thus represent more profitable food resources (Baldassarre & Bolen, 2006). Birds will rarely consume an entire plant, often foraging selectively on specific tissues (O'Hare *et al.*, 2007; Rodriguez-Villafane *et al.*, 2007). Several factors have been shown to influence palatability, both of tissues and species, to foraging waterfowl. The nutritional quality is an important factor in determining what a bird will consume (Cebrian & Lartigue, 2004). Energy content and digestibility of the plant tissue, which determine the metabolisable energy available to the forager, typically influence waterfowl preferences. In order to maximise fitness waterfowl should seek to maximise their rate of metabolisable energy gain; *i.e.* 'rate maximisation', the amount of energy gained minus the metabolic costs of foraging per unit time (Stephens &

Krebs, 1986; Nolet *et al*., 2002; Gyimesi *et al*., 2012). Plant seeds are preferentially foraged by species of goose and duck as they represent a discrete, energy-rich food resource (Ely, 1992; Combs & Fredrickson, 1996). Nitrogen may also be a limiting nutrient for birds that are largely herbivorous as plant material is low in nitrogen relative to avian body tissue; thus individuals may select plant material with the highest available nitrogen content (Mattson, 1980; Sedinger, 1997; Fox *et al.*, 1998; Durant *et al.*, 2004). Whilst much research indicates that nutritional quality is the principle determinant of waterfowl food selection, several studies have demonstrated that secondary metabolite compounds in plant tissues can substantially decrease palatability to waterfowl (Buchsbaum *et al.*, 1984). Secondary metabolites, such as alkaloids and phenolic compounds, are more common among freshwater macrophytes than previously estimated, but are still less prevalent than in many terrestrial plant groups (Prusak *et al.*, 2005). How freshwater macrophyte tensile strength affects herbivore foraging is not well understood, although it may be important in coastal ecosystems, where some species of macroalgae increase tissue strength and toughness as an induced response to herbivore damage (Lowell *et al.*, 1991). O'Hare *et al.* (2007) reported that water crowfoot tissues grazed selectively by swans required only one-third of the force to remove compared with ungrazed tissues. Greater tensile strength is likely to increase the costs associated with foraging, and reflect a higher percentage of relatively-indigestible structural tissues.

The importance of waterfowl grazing of terrestrial plants has been long-established, whereas in aquatic ecosystems the importance has received growing recognition only in recent decades (Lodge, 1991; Klaassen & Nolet, 2007). There is a growing body of evidence of waterfowl effects on plants and wider ecosystems. Waterfowl can cause reductions in plant abundance of up to 100 % in extreme cases (Lodge *et al*., 1998; Marklund *et al*., 2002). Waterfowl have been shown to reduce plant abundance in a range of habitats, typically at equal or greater magnitudes than other plant-consuming taxa (Lodge *et al*., 1998). Despite such evidence, many recent limnology textbooks still do not discuss waterfowl herbivory and its roles in aquatic ecosystems (*e.g.* Lampert & Sommer, 2007).

There is a pressing need to improve our understanding of waterfowl-plant interactions as many species of plant-eating waterfowl have increased recently. For example, mute swan populations have risen in many regions including Britain (Ward *et al*., 2007), Central Europe (Musil & Fuchs, 1994; Gayet *et al*., 2011a), Fenno-Scandinavia (Nummi & Saari, 2003), the Netherlands (van Eerden *et al*., 1996) and North America (Petrie & Francis, 2003). Of the 21 goose species (*Anser spp*. and *Branta spp*.) for which long-term population trends in Europe are known, 16 are increasing (Fox *et al*., 2010). European

populations of some species of dabbling ducks, such as Eurasian wigeon (*Anas penelope* L.) and gadwall (*Anas strepera* L.) have also increased over recent decades (van Eerden *et al*., 1996).

1.4 Grazing conflicts

In many instances herbivory is a desirable process in the maintenance of the diversity, structure, functioning and service provision of ecosystems (van Wieren & Bakker, 1998; Klaassen & Nolet, 2007; Hodder & Bullock, 2009; Taylor, 2009). However, where waterfowl or other herbivores have an effect on plant communities that has undesirable ecological (*e.g.* loss of biodiversity) or socioeconomic (*e.g.* reduced crop yield) consequences, this can be termed a 'grazing conflict'. Of particular concern are the grazing conflicts between waterfowl and agriculture due to the potential for economic losses (Baldassarre & Bolen, 2006). Waterfowl consumption of crops is not a modern phenomenon (Kear, 2001), however losses of traditional aquatic feeding habitats and increases of intensive agriculture in the last century have led to increased waterfowl feeding on agricultural land (Baldassarre & Bolen, 2006). A variety of agricultural crops are consumed, including oilseed rape, rice, sugar beet, improved grassland, and winter cereals such as wheat and barley (Lane *et al.*, 1998; Parrott & McKay, 2001a; Colhoun & Day, 2002). Cereal grains in particular represent a profitable food resource with a high energy content and low handling time relative to leafy vegetation (Baldassarre & Bolen, 2006). Complaints against waterfowl include consumption and trampling of crops causing yield loss, and faecal contamination causing decreased crop palatability. Yield losses can be substantial; foraging Eurasian wigeon reduced yields of winter wheat by 83 % in five fields near Misato City, Japan (Lane & Nakamura, 1996). Most reports of crop damage relate to geese, with substantial variation in yield reduction based on crop species, weather, flock size, farming practices, and time of year (Bedard *et al.*, 1986; Summers, 1990; McKay *et al.*, 1993). Swans have also been implicated in winter crop damage; mute swans (*Cygnus olor* Gmelin, 1789) reduced yields of oilseed rape by up to 24 % in a study in England (Parrott & Watola, 2007), whilst whooper swans (*Cygnus cygnus* L.) reduced yields of improved grass by up to 65 % in fields in northwest Ireland (Colhoun & Day, 2002). However, yield losses due to waterfowl herbivory are generally considered to be a localised problem. Most waterfowl utilise agricultural land in small numbers and for short durations; winter foraging by mute swans on arable crops in England has been estimated to involve only 3 % of the total population, concentrated in east and south-east England (Rees *et al.*, 1997). However, as losses to individual farmers can be substantial, some countries operate compensation schemes or authorise culls; the Netherlands cull

approximately 25 % of the mute swan population per annum, but continue to experience grazing conflicts (Esselink & Beekman, 1991).

Grazing conflicts also occur where herbivores have negative effects on biological communities of conservation importance. Such conflicts often occur where plants, which support diverse and abundant secondary production, are depleted by grazing (Trump, 1996; Tatu *et al*., 2007; Newson *et al*., 2012). Grazing damage by herbivores may prevent the exploitation of that habitat by species of conservation importance (*e.g.* Vickery *et al*., 1997). Alternatively, the plants themselves may be of high conservation value directly, such as a rare species (Duka & Masters, 2005; Ancheta & Heard, 2011). The consequences of such grazing conflicts may be localised depletion, or in exceptional cases extirpation, of the ecologically valuable plants and their associated fauna and epiphytic flora (Côté *et al*., 2004; O'Hare *et al*., 2007; Dolman *et al*., 2010).

1.5 The management of herbivores and their effects

As herbivores can cause ecological and socioeconomic damage through their interactions with plants, there is frequently a need to alleviate grazing conflicts to prevent or reduce such damage. In most instances the aim of management is not to prevent all herbivory, but alleviate the negative effects of herbivory. Only in the case of exotic species is the complete elimination of the herbivore population ever a desired option (*e.g.* Ellis & Elphick, 2007). Management of grazing conflicts may involve habitat alteration, manipulations of herbivore populations or predator densities, feeding deterrents such as chemical repellents, scaring, physical barriers such as fences, or financial compensation for grazing damage (Vickery *et al*., 1994; Hake *et al*., 2010). Changes in local habitat management have become an increasingly common approach to alleviate grazing conflicts. For example, plant stands and associated biota could be protected by the establishment of sacrificial feeding areas near to areas of overgrazing; if the sacrificial crop plants are more profitable to the forager, in terms of gain of energy or nutrients, foragers are likely to consume these sacrificial plants in preference to those managers wish to protect (Owen, 1977; Vickery *et al*., 1994; Amano *et al.*, 2007). Sacrificial feeding areas have been used to successfully alleviate a swan grazing conflict with agriculture in the River Tweed catchment in Scotland (Spray *et al*., 2002). However, herbivore population control has traditionally focused on reducing the number of individuals in an area over a period of time through translocation (Hodder & Bullock, 1997; Duka & Masters, 2005) or culling (Middleton *et al*., 1993; Ellis & Elphick, 2007), or on reducing reproductive output through fertility control (Brooks *et al*., 1980; Duka & Masters, 2005;

Williams *et al.*, 2007) or, in birds, destroying eggs (Wright & Phillips, 1991; Watola *et al.*, 2003). Selecting appropriate methods of population control requires consideration of the ecological, economic, and ethical consequences of control (Duka & Masters, 2005; Minteer & Collins, 2005; Ellis & Elphick, 2007). Such techniques can be expensive, in terms of time and effort required, and care must be taken to ensure that the costs of management do not exceed the costs of herbivore damage, particularly where other management options exist (Vickery *et al*., 1994). The manipulation of animal populations has become an increasingly emotive issue, particularly where lethal methods are used or target species are 'charismatic' (*i.e.* popular with the public) (Sladen, 1991; Nolet & Rosell, 1998; Perry & Perry, 2008). Thus managers must ensure that methods of population control are likely to achieve the desired ecological outcomes, are cost effective, and that more ethical methods do not provide a reasonable alternative management strategy. Identifying the most suitable management option is further hindered by the fact that the literature on management is fragmented and is often based on small-scale studies with little post-treatment monitoring.

1.6 The role of modelling in plant-herbivore interactions

To avoid wasted effort and needless controversy it may be necessary to evaluate the chances of any proposed management strategy achieving a defined objective. Ecological models, which simulate the behaviours and responses of individuals and populations from simple rules, provide a means of conducting such evaluations. For example, mathematical population models predict changes in population sizes over time based on processes which influence the rates of births, deaths, immigration and emigration (Caswell, 2001). Such population models have proven powerful tools for the prediction and evaluation of the consequences over time of management decisions on species abundances and distributions (Middleton *et al*., 1993; Caswell, 2001); thus such models could be used to test the effects of different management options on the level of grazing conflict observed in an area.

Alternatively, the movements and feeding behaviours of herbivores can be simulated using individual-based models (IBMs), which predict the movements of individual animals within a population on the basis that foragers attempt to maximise their perceived fitness (Grimm & Railsback, 2005; Stillman & Goss-Custard, 2010). The rate of energy gain is typically used as a proxy for fitness, due to the difficulty of measuring lifetime reproductive success (Stephens & Krebs, 1986). A wide range of field tests have demonstrated that differences in net energy gain explain the diets and distributions of

organisms (Owen-Smith & Novellie, 1982; Nolet *et al*., 2001; Sih & Christensen, 2001; Killen *et al*., 2007; Babin *et al*., 2011). IBMs have previously been used to test management strategies to resolve a wide range of wildlife conflicts, such as those between geese and agricultural crops, large felids and human livestock, and between shorebirds and shellfisheries (Ahearn *et al*., 2001; Stillman *et al*., 2001; Stillman *et al*., 2003; Amano *et al*., 2004). Such successes indicate that IBMs could be used to test the likely effectiveness of different management options for the alleviation of the swan grazing conflict in chalk rivers. As with all ecological models, IBMs must (i) be explained clearly so as to be understandable and replicable, (ii) be subjected to sensitivity analyses that quantify how predictions change when parameters values are varied, and (iii) have their predictions tested against field data, in order to assess the degree of confidence which both researchers and managers can have in the model predictions (Bart, 1995; Grimm & Railsback, 2005). Whilst mathematical population models and individual-based models are not the only available ecological models, they represent two of the most promising approaches in advising the management of grazing conflicts (Middleton *et al*., 1993; Stillman & Goss-Custard, 2010).

1.7 The chalk river ecosystem

Chalk river ecosystems have been, and remain, heavily managed for the purposes of agriculture, conservation and sport fishing (Environment Agency, 2004). As such, they are attractive, plant-rich habitats that support abundant and diverse wildlife (**Figure 1.2**). Much of the land adjacent to a river channel is devoted to pastoral farming and the river was traditionally managed to facilitate flooding of these fields at certain times of year to improve the growth of grasses for livestock (Bettey, 1999). Whilst this practice has declined in recent decades the numerous side streams and ditches, created to achieve this seasonal flooding, remain. The pasture grass community is managed so that these species remain dominant, as they are sown for their use as food for livestock (Bettey, 1999). Within such catchments there are small patches of damp woodland of Black Alder (*Alnus glutinosa* L.) and Willow (*Salix spp.*). The rivers themselves typically consist of a main channel with numerous side streams, known as ‘carriers’, which branch off and rejoin the main channel further downstream.

Figure 1.2: *A typical chalk river reach, showing the river channel dominated by water crowfoot and the surrounding terrestrial pastures. Note the dense growth and abundant white flowers of water crowfoot.*

The relatively stable environmental conditions of these low turbidity, groundwater-fed rivers facilitates both their use by humans and a highly productive ecological community (Berrie, 1992; Environment Agency, 2004). Groundwater emerging from the chalk aquifer is typically 11 °C (Crisp *et al*., 1982). These substantial groundwater inputs have a warming effect in winter and cooling effect in summer, with the result that chalk river temperatures rarely fall below 5 °C or climb above 17 °C (Mackey & Berrie, 1991). Thus a relatively stable water temperature is achieved regardless of fluctuations in air temperature (Berrie, 1992; Arnott, 2008). Groundwater from the chalk aquifer has a relatively stable chemical composition, with a high ionic content due to calcium bicarbonate and a pH in the range 7.4-8.0 (Berrie, 1992). The seasonal range of water velocities can span an order of magnitude, from 0.1 to over 1.0 m s^{-1}, being greatest in winter and lowest in autumn (Dawson, 1976b). Water retention time varies between one and seven days, being higher in longer, slower rivers (Dawson, 1976b).

The chalk rivers of southern and eastern England are of high conservation value. Chalk rivers support high abundances of invertebrates and fishes, in particular salmonid species

such as brown trout (*Salmo trutta* L.) and Atlantic salmon (*S. salar* L.) (Berrie, 1992; Environment Agency, 2004). Chalk rivers can also support species of international conservation importance, such as the Eurasian otter (*Lutra lutra* L.), sea lamprey (*Petromyzon marinus* L.) and white-clawed crayfish (*Austropotamobius pallipes* Lereboullet, 1858) (Environment Agency, 2004). High salmonid abundances, coupled with the high aesthetic quality of chalk river, support economically valuable game fisheries (Ladle & Westlake, 1976). The high aesthetic quality of chalk river catchments also makes them popular for other outdoor activities, such as canoeing, rambling and bird watching (Ladle & Westlake, 1976; Environment Agency, 2004). The ecological and socioeconomic value of chalk rivers is due in part to the high abundances of submerged macrophytes which increases physical wetted volume of the river and provides habitat, shelter and food for other organisms (Dawson, 1976b; Hearne & Armitage, 1993; Armitage & Cannan, 2000). In chalk rivers the macrophyte community is typically dominated by stream water crowfoot *Ranunculus penicillatus ssp*. *pseudofluitans* (hereafter 'water crowfoot'), a perennial, submerged macrophyte with flexible stems and capillary leaves that can extend over 2 m downstream from the roots (Dawson, 1976a). Previous studies have shown that invertebrate densities are greater for macrophyte stands relative to unvegetated substrates (Wright *et al*., 1983; Wright, 1992; Tod & Schmid-Araya, 2009). Reduced production of submerged macrophytes results in lower invertebrate production and diversity, as well as reduced salmonid population densities and individual body size (Riley *et al*., 2009). In recognition of the keystone role of water crowfoot in sustaining a diverse ecosystem of high productivity and conservation value, the plant is protected under the EU Habitats and Species Directive (92/43/EEC).

Macrophytes exhibit seasonal cycles of growth and recession; growth is strong in spring (April-June), peak abundances are reached in July and declines occur thereafter (Owens and Edwards, 1961; Dawson, 1976a). Water crowfoot typically flowers between April and June, with sites further downstream flowering later than sites further upstream (Dawson, 1980). Peak biomass can range between 200 and 1500 g DM m^{-2}, being generally lower in smaller rivers (Owens & Edwards, 1961; Dawson, 1976a; Ham *et al*., 1981; O'Hare *et al*., 2007). Many chalk rivers lack dense riparian vegetation, due to livestock grazing and clearance for sport fishing, thus much of the primary productivity is autochthonous (Dawson, 1976b). Winter discharge, which is typically five times greater than the summer and autumn (Armitage & Cannan, 2000; Bowes *et al*., 2005), removes large quantities of plants and prevents regrowth above a maximum biomass. Key factors that regulate chalk river plant community structure and function are water temperature (Dawson *et al*., 1981) and light availability (Dawson, 1976a; Dawson, 1976b). At depths exceeding 0.35 m, macrophyte biomass is known to be negatively related to depth as a consequence of reduced light availability (Dawson, 1976a). Water flow is also a key factor regulating plant abundance as photosynthetic rates increase with water velocity (Westlake *et al*., 1967).

Concentrations of growth-limiting nutrients are known to influence plant species interactions and dominance (Spink *et al.*, 1993); however, most chalk rivers are enriched due to agricultural run-off and treated sewage from human settlements and thus such nutrients are highly abundant and are are not thought to limit macrophyte growth (Casey & Downing, 1976; Kern-Hansen & Dawson, 1978; House *et al*., 2001; O'Hare *et al*., 2007). Recent research has also suggested that herbivory by swans can limit macrophyte abundance (O'Hare *et al*., 2007). Concerns have been raised by riparian stakeholders regarding damage to both pasture grasses and aquatic plants by flocks of swans (Harrison, 1985; Trump *et al*., 1994; Sayers & Walsha, 1996; O'Hare *et al*., 2007; Porteus *et al*., 2008). Swan flocks are comprised of juveniles and non-breeding adults (Minton, 1971). Harrison (1985) demonstrated a mean pasture grass yield loss of 11.4 % in fields grazed by flocks of swans, increasing livestock feed costs for the farmers affected. O'Hare *et al*. (2007) reported a 49.2 % reduction in aquatic plant biomass due to grazing by a flock. Losses of aquatic plants due to grazing are known to reduce the value of river reaches as sport fisheries (Fox, 1994). Given these negative ecological and socioeconomic effects of swan grazing, there is a need to alleviate the grazing conflict through management.

Mute swans are the principle herbivore of aquatic plants in chalk river catchments and the only species considered capable of causing depletion of macrophytes, due to the higher densities and greater consumption and trampling of swans relative to the few other aquatic herbivores present (Sayers & Walsha, 1996; Trump, 1996; O'Hare *et al*., 2007). The only fish species common to chalk rivers which consumes living plant tissues is the dace (*Leuciscus leuciscus* L.), although plants generally comprise only a small fraction of their diet (Davies *et al*., 2004). Dace densities are considered too low to cause depletion of macrophytes (Garner & Clough, 1996; Clough & Ladle, 1997; Clough *et al*., 1998).

1.8 Mute swan ecology

The mute swan is a large herbivorous bird native to the western Palaearctic, but has also been introduced to North America, South Africa, Australia and Japan (Birkhead & Perrins, 1986; Kear, 1988; **Figure 1.3**). In Great Britain the mute swan population has undergone a substantial increase from 17,600 individuals in 1978 to 31,700 in 2002, and is believed to have continued rising since (Ward *et al*., 2007). Several factors are believed to have contributed to this increase. Firstly, agricultural intensification and the switch to sowing of fertiliser-enriched winter crops has increased the availability of high-quality food during winter, which has decreased mortality at this physiologically-demanding time of years

(van Eerden *et al*., 1996). Secondly, the phasing-out of lead weights in angling during the late 1980s removed a major cause of mortality, as swans previously ingested lead weights alongside grit (an aid to digestion) and suffered lethal poisoning (Birkhead & Perrins, 1986; Kear, 1988). Thirdly, the passing of the 1981 Wildlife and Countryside Act in the UK resulted in reduced persecution of swans by man (Birkhead & Perrins, 1986). Other local factors may have also contributed to the population increase, such as the use of deflector discs on power cables to reduce mortality due to collisions (Perrins & Sears, 1991). However, to date there has been no analysis of the relative importance of such factors in the mute swan population increase. Few animals in Britain can kill a swan and thus predation risk is minimal, accounting for just 3.4 % and 5.4 % of annual mortality of adults and juveniles respectively (Brown *et al*.,1992). Mute swans are native to Britain, where they are resident throughout the year (Birkhead & Perrins, 1986; Kear, 1988). Mute swans are popular with the public and are thus referred to as a 'charismatic species' (Sladen, 1991; Ellis & Elphick, 2007). Swans are protected under the EU Wild Birds Directive (2009/147/EEC), implemented in the UK through the Wildlife and Countryside Act (1981), making it illegal to capture, kill or injure swans, or to disturb or damage nests or eggs.

Figure 1.3: *A flock of mute swans caught during the annual round-up for leg ringing, July 2010. Note the differences in bill colouration, with orange bills indicating adults and pinkish-grey bills indicating juveniles. Photograph courtesy of the Radipole Ringing Group.*

Mean adult weight is 10.8 kg, with males typically heavier than female (Birkhead & Perrins, 1986; Delany, 2005). Contrary to popular legend the mute swan is not the heaviest flying bird, a distinction belonging to the male great bustard (*Otis tarda* L.) at 13.5 kg (Dunning Jr., 1992). Nor are they the largest species of swan, as the trumpeter swan (*Cygnus buccinator* Richardson, 1832) weighs on average 12.0 kg as an adult (Kear, 2005). Mute swans can live for up to 30 years in the wild, although average age is typically around 7 years (Birkhead & Perrins, 1986; Coleman *et al*., 2001). Mute swans are capable of breeding from two years of age, but competition for territories (which are won by heavier, older males) means that most individuals do not reproduce until they are four years old (Birkhead & Perrins, 1986; Trump *et al*., 1994). Despite mute swans being a sexually dimorphic species, sex determination in wild swans is difficult through observational methods. Whilst relative bill knob size is typically larger in males, knob size in both males and females varies with season and body condition, making it an unreliable trait with which to determine sex (Horrocks *et al*., 2009). Breeding swans are territorial, excluding all other individuals from an area that varies in size according to food quality, channel morphology and the number of other swans in the area (Scott, 1984; Trump *et al*., 1994; Parrott & McKay, 2001b). Nests consisting of mounds of aquatic vegetation are built in mid-March, with young born after a 36 day incubation period (Delany, 2005). Clutch sizes can range between 1 and 10 eggs, with 6 eggs a mean clutch size (Perrins & Reynolds, 1967; Coleman *et al*., 2001; Watola *et al*., 2003). Young (termed 'cygnets') fledge (*i.e.* become 'juveniles') within 120-150 days depending on growth rate, and are typically chased away by their parents in the autumn or winter, from September onwards (Delany, 2005). These juveniles often join flocks of other young and non-breeding adult swans (Minton, 1971).

Swans in chalk river catchments exploit a range of habitats, including river, pasture and arable fields, gravel pits and natural lakes, ditches and estuaries (Trump *et al*., 1994). However, most swans have been observed on the main river channel where they consume aquatic plants, or in pasture fields where they consume terrestrial grasses (Trump *et al*., 1994; Trump, 1996). The mute swan is a generalist herbivore, consuming a wide range of submerged and emergent macrophytes and terrestrial plants (Birkhead & Perrins, 1986; Bailey *et al*., 2008). Mute swans can forage up to 0.8 m below the surface using just their necks and up to 1.0 m by 'upending' (Owen & Cadbury 1975; **Figure 1.4**). As chalk rivers are typically < 1.0 m in depth (Berrie, 1992), macrophytes lack depth refugia to avoid herbivory as in some other ecosystems (Santamaria & Rodriguez-Gironés, 2002).

Figure 1.4: *Two adult mute swans on a chalk river reach. The swan in the background is demonstrating their primary mode of foraging, submerging their neck below the surface to graze aquatic plants.*

Several other swan species may be observed in the chalk river catchments of southern and eastern England; the overwintering Bewick's and whooper swans and the non-native black swan (Prendergast & Boys, 1983; Liley *et al*., 2008). However, these typically occur in small numbers and no reports of grazing conflicts have been reported for these species in chalk rivers (Sayers & Walsha, 1996; Trump *et al*., 1994; Trump, 1996; Watola *et al*., 2003; O'Hare *et al*., 2007).

1.9 The study system: The River Frome (Dorset, UK)

The River Frome catchment is situated in the county of Dorset, close to the southern coast of Britain (**Figure 1.5**). The River Frome arises in Evershot (50°50'N, 02°36'W) before flowing 143.3 km through Dorset (UK), discharging into the English Channel via Poole Harbour (50°43'N, 02°02'W). Within a catchment of 414 km^2 the River Frome receives several smaller tributaries, principally the River Piddle, River Hooke, River Cerne and Tadnoll Brook, but these small rivers do not alter the major characteristics of the River Frome (Bowes *et al*., 2005; Arnott, 2008). The river is a shallow (typically < 1 m depth), mesotrophic chalk river with a predominantly gravel and sand substrate (Bowes *et*

al., 2005; O'Hare *et al*., 2007; Sievers, 2012). Land use in the catchment is dominated by arable (44 %) and pastoral (37 %) agriculture, with lower coverage of woodland (11 %), heath (3 %) and urban areas (5 %) (Arnott, 2008).

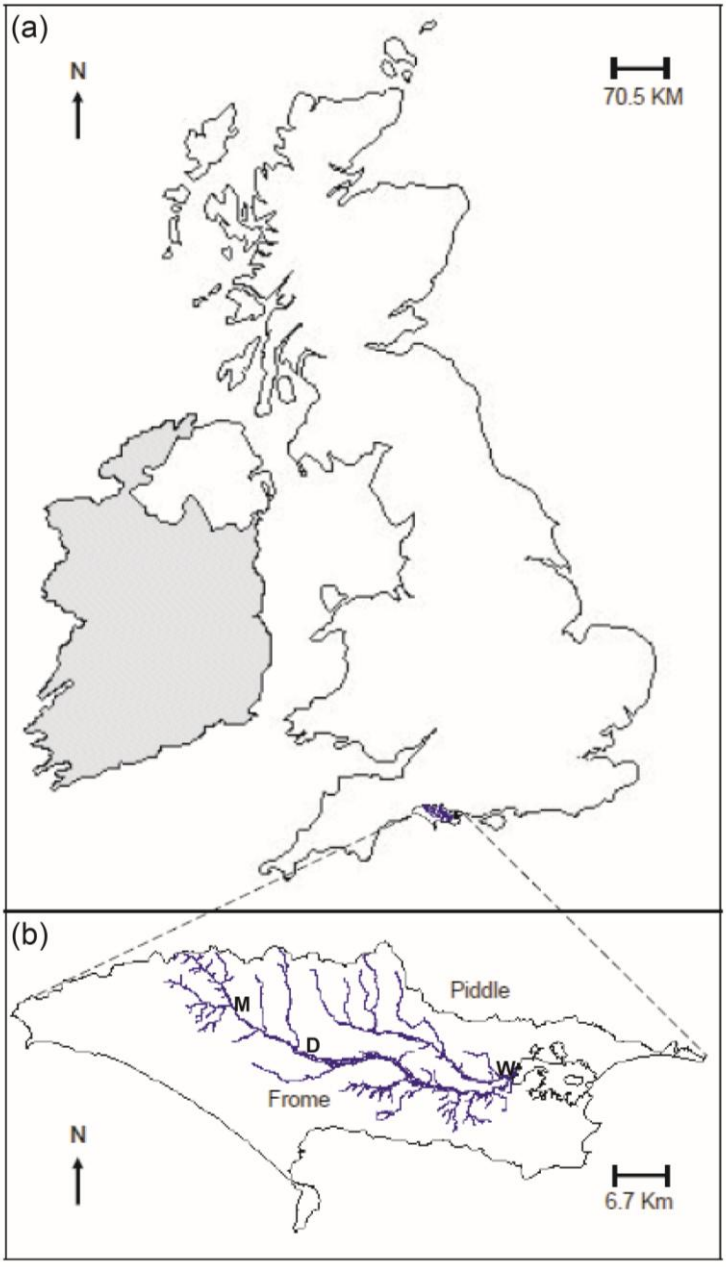


Figure 1.5: *Two maps showing (a) the location of the River Frome catchment within the United Kingdom, and (b) the River Frome catchment itself. The main tributary, the River Piddle, is also indicated. Letters refer to major settlements; M = Maiden Newton, D = Dorchester, W = Wareham. Modified from Arnott (2008).*

Annual mean soluble reactive phosphorus concentration in the main river is 88 µg l^{-1} (Bowes *et al*., 2009), which exceeds the 60 µg l^{-1} target for chalk rivers set by the Environment Agency (Mainstone & Parr, 2002). Annual mean nitrate concentration in the main river is 7.0 mg NO_3-N l^{-1}, which is currently below the legal upper limit set by the European Union Nitrates Directive (Howden & Burt, 2009).

The pasture field plant community is dominated by a small number of grass species, typically perennial ryegrass (*Lolium perenne* L.), creeping bentgrass (*Agrostis stolonifera* L.), and Yorkshire fog (*Holcus lanatus* L.) (Allison Stillman, Dorset Environmental Records Centre, personal communication). The aquatic plant community is dominated by water crowfoot, with smaller quantities of perfoliate pondweed (*Potamogeton perfoliatus* L.), Canadian pondweed (*Elodea canadensis* Michx.), horned-pondweed (*Zannichellia palustris* L.), blunt-fruited starwort (*Callitriche obtusangula* Le Gall), European bur-reed (*Sparganium emersum* Rehmann), river water-dropwort (*Oenanthe fluviatilis* Coleman), watercress (*Nasturtium officinale* Aiton), and Eurasian water milfoil (*Myriophyllum spicatum* L.) also present in greater abundances at sites further from the river source (Dawson, 1976a; Dawson, 1976b; O'Hare *et al*., 2007). In recognition of the abundant and diverse biota supported (see **Section 1.7**), the River Frome has been designated a Site of Special Scientific Interest (SSSI) between Dorchester (50°43'N, 02°26'W) and Wareham (50°41'N, 02°05'W).

A major advantage of carrying out a research project within the River Frome catchment is the wealth of background information which can be utilised, potentially saving time and effort in data collection and increasing the understanding of the wider ecosystem in which the study organisms exist. The presence of a number of research facilities and environmental organisations within the catchment, in particular the East Stoke River Laboratory of the Freshwater Biological Association, means that the River Frome and its tributaries represent one the most comprehensively studied river catchments in the world. Long term monitoring of catchment hydrology and nutrient dynamics has been undertaken (Hanrahan *et al*., 2001; Bowes *et al*., 2005). The various components of the ecological community have received much attention, including plants (Dawson, 1976a; Cotton *et al*., 2006; Gurnell *et al*., 2006; Wharton *et al*., 2006; O'Hare *et al*., 2007), meiofauna (Sleigh *et al*., 1992; Woodward *et al*., 2008), macroinvertebrates (Dawson *et al*., 1991; Armitage & Cannan, 2000; Harrison & Harris, 2002; Wharton *et al*., 2006), fish (Mann, 1989; Ibbotson *et al*., 1994; Garner & Clough, 1996; Prenda *et al*., 1997; Clough *et al*., 1998), and birds (O'Hare *et al*., 2007; Liley *et al*., 2008). Thus a wealth of data are already available for any ecological study in the River Frome catchment.

Based on the maximum monthly overwinter counts given by Liley *et al*. (2008), the River Frome waterfowl community is numerically composed mostly by northern mallard *Anas platyrhynchos* L. (37.9 %), mute swan (21.6 %), Eurasian teal *Anas crecca* L. (16.1 %) and Eurasian wigeon *Anas penelope* L. (13.0 %), with the latter two species largely confined to the estuary (**Figure 1.6a**). This pattern of dominance by mallard and mute swans has been reported for other British lowland rivers and reflects their national widespread abundances (Mason & Macdonald, 2000). However, in terms of biomass the River Frome waterfowl community is dominated by mute swans (72.1 %) (**Figure 1.6b**). Recent evidence has suggested that waterfowl biomass is a better determinant of the strength of herbivore-plant interactions (Gyimesi *et al*., 2011); this idea will be tested in this thesis (**Chapter 2**). Therefore in the River Frome mute swans are likely to dominate waterfowl-plant interactions. In addition to their lower biomasses, the foraging of mallard and other small-bodied waterfowl appears limited to surface dabbling on drifting seeds and invertebrates in the slower-flowing margins and ditches rather than subsurface foraging on submerged macrophytes in the main channel (K.A. Wood, personal observation). Accordingly, whilst concerns have been raised by riparian stakeholders regarding swan grazing of macrophytes, no complaints regarding other species have been reported (Sayers & Walsha, 1996; Trump, 1996).

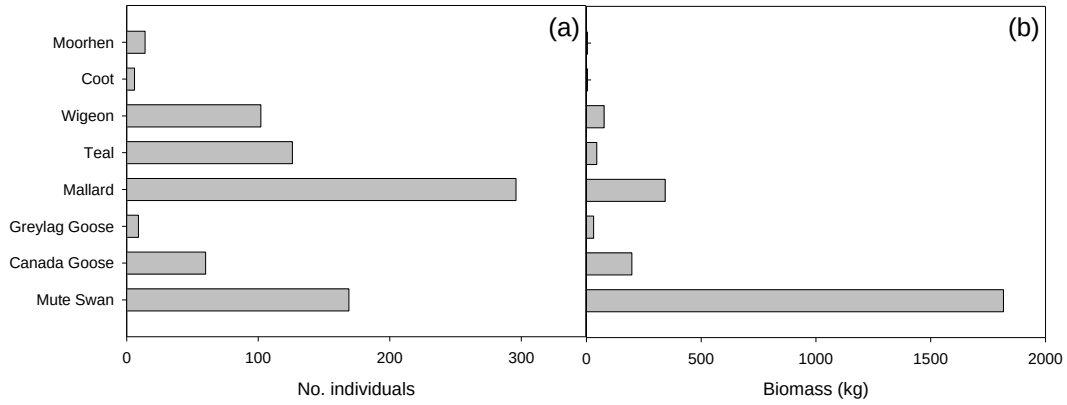


Figure 1.6*: The composition of the River Frome waterfowl community based on (a) numbers of, and (b) total biomass of, each species. Numbers of each species were reported in Liley* et al*. (2008), whilst biomass values were given in Kear (2005).*

Historically, studies of mute swans in Dorset have focused on the colonially-breeding population at Abbotsbury and the Fleet lagoon, which is largely a closed population (Perrins & Ogilvie, 1981; McCleery *et al*., 2002). Few data exist for the inland populations which use the chalk rivers and associated habitats. Prendergast & Boys (1983) state that "sizeable flocks occur in the river valleys in some winters", but offer no quantitative information. A small number of occasional winter ornithological surveys have been carried out in the lower Frome catchment, covering the 19.4 km section between Wool and Poole Harbour. A comparison of these surveys carried out in the lower Frome catchment (Liley *et al*., 2008) indicates that the overwintering population of mute swans in the area has increased since at least the early 1990s (Linear regression: $F_{1,4} = 1037.6$; $p < 0.0001$; $R^2_{adj} = 100$ %; **Figure 1.7**).

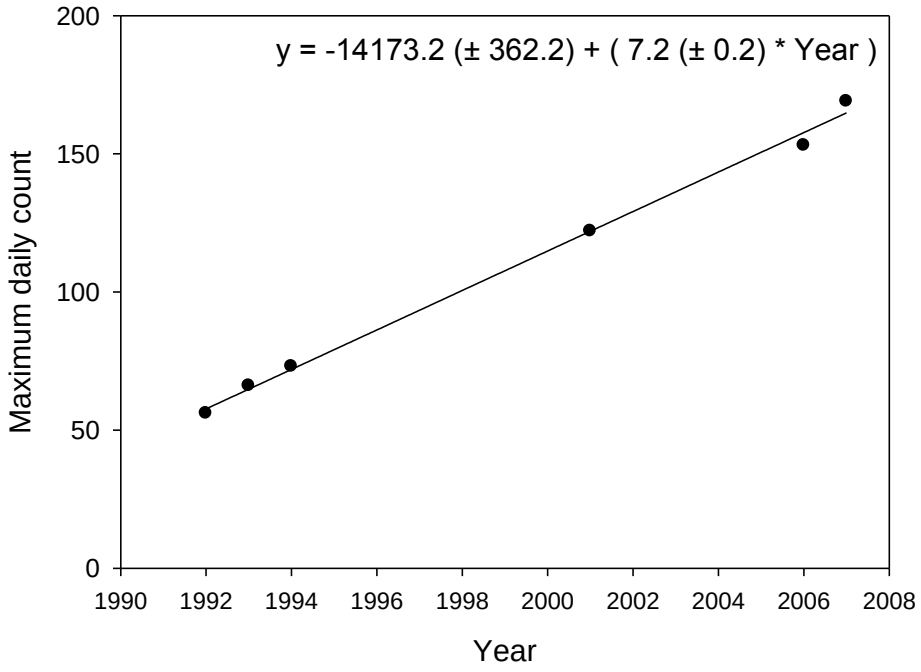


***Figure 1.7**: The maximum daily numbers of mute swans reported during the winter (October to March) period, based on six historical surveys of the lower Frome catchment.*

1.10 Thesis overview

This thesis examines three main topics in swan-plant interactions. The first topic, examined in chapters 2 and 3, addresses two unresolved questions of how swan-plant interactions should be quantified. **Chapter 2** uses a meta-analysis approach to test whether waterfowl numerical densities (ind. ha^{-1}) or biomass densities (kg ha^{-1}) are

closely related to reductions in plant abundance. **Chapter 3** considers how plant abundance can be quantified efficiently and the relatedness of different measures of abundance. The insights of chapters 2 and 3 are then used to inform the second main topic of the thesis, which examines the spatiotemporal variance in the grazing conflict between swans and macrophytes. To address this second topic **Chapter 4** quantifies the effects of swan herbivory relative to three other factors known to affect plants (riparian shading, water temperature and distance from river source) on a suite of plant community properties. The third topic of the thesis, which has the greatest number of chapters devoted to it due to the relative lack of previous research in this area, focuses on how grazing conflicts can be managed efficiently and ethically. There was a lack of available swan population data at the catchment-scale with which to address management questions. Thus **Chapter 5** quantifies the seasonal variation in the structure, reproduction and habitat use of a chalk river population. **Chapter 6** uses these data to construct and test a population model for the River Frome. This model is used to explore the effectiveness of population control as a means of alleviating the grazing conflict. A second management strategy is also explored; the exploitation of the ability of swans to switch habitats in response to changing food profitability to move the swan flocks away from valuable macrophytes or crops. **Chapter 7** identifies the mechanism which regulates behavioural decisions and drives such habitat shifts. **Chapter 8** constructs and tests an individual-based model and uses this to test different management options for alleviating the grazing conflict, based around the key concept of habitat switching. Finally, the conclusion (**Chapter 9**) examines the advances in the understanding of plant-herbivore interactions made in this thesis. Future priorities for both research and policy are identified.

Chapter 2: The impact of waterfowl herbivory on plant standing crop: a meta-analysis.

2.1 Abstract

Waterfowl can cause substantial reductions in plant standing crop, which may have ecological and economic consequences. However, what determines the magnitude of these reductions is not well understood. Using data from published studies, I derived the relationship between waterfowl density and reduction in plant standing crop. When waterfowl density was estimated as individuals ha^{-1} no significant relationship with reduction in plant standing crop was detected. However, when waterfowl density was estimated as kg ha^{-1} a significant, positive, linear relationship with reduction in plant standing crop was found. Whilst many previous studies have considered waterfowl species as homologous, despite large differences in body mass, my results suggest that species body mass is a key determinant of waterfowl impact on plant standing crop. To examine relative impacts of waterfowl groups based on species body mass, a measure of plant biomass reduction (R_s) per bird per hectare was calculated for each group. Comparison of R_s values indicated some differences in impact between different waterfowl groups, with swans having a greater *per capita* impact than smaller-bodied waterfowl groups. I present evidence that this difference is linked to disparities in individual body size and associated differences in intake rates, diet composition and energy requirements. Future research priorities are proposed, particularly the need for experiments that quantify the importance of factors that determine the magnitude of waterfowl impacts on plant standing crop.

2.2 Introduction

The quantity of living plant tissues in a given area, typically defined as 'standing crop', affects ecosystem structure, functions and service provision (Grime, 2002). Herbivores can have substantial effects on plant standing crop in aquatic ecosystems (Lodge, 1991; Newman, 1991), which may have ecological and socioeconomic consequences (Baldassarre & Bolen, 2006; Klaassen & Nolet, 2007; Elmberg, 2009). Such impacts may in turn cascade onto other organisms which use plants (*e.g.* Sammler *et al.*, 2008; Samelius & Alisauskas, 2009). Published estimates of waterfowl reductions in plant standing crop range between 0–100% (Lodge *et al.*, 1998; Marklund *et al.*, 2002; Badzinski *et al*., 2006; Rodríguez-Pérez & Green, 2006; O'Hare *et al*., 2007), yet what determines the magnitude of such reductions is unclear. In particular, how reductions in plant standing crop are related to waterfowl densities is not understood, yet much of the

management of waterfowl in high value plant habitats assumes that reductions in plant standing crop will be lessened by reducing waterfowl densities (Ankney, 1996; Baldassarre & Bolen, 2006). There is a pressing need to improve my understanding of waterfowl impacts on plant standing crop as many species of waterfowl herbivores have increased recently. For example, mute swan (*Cygnus olor* Gmelin, 1789) populations have risen in many regions including Britain (Ward *et al*., 2007), Central Europe (Musil & Fuchs, 1994; Gayet *et al*., 2011a), Fenno-Scandinavia (Nummi & Saari, 2003) and North America (Petrie & Francis, 2003). Of the 21 goose species (*Anser spp*. and *Branta spp*.) for which long-term population trends in Europe are known, 16 are increasing (Fox *et al*., 2010). Most reports of waterfowl damage to plants concern consumption, trampling, and faecal deposition (Ankney, 1996; Baldassarre & Bolen, 2006; Elmberg, 2009). These impacts have led to widespread human-waterfowl conflicts and management interventions including protection of plants using fenced enclosures and controlling of waterfowl populations through culls and egg destruction (Wright & Phillips, 1991; Haramis & Kearns, 2007).

In this study, I used published values to test the relationship between waterfowl density and reductions in standing crop. Differences in plant standing crop associated with and without herbivores do not represent solely plant consumption or removal. For example a number of positive and negative feedback mechanisms, such as the stimulation of plant growth by the elevation of nutrient concentrations by herbivore faecal deposition, can also influence changes in plant standing crop (Mitchell & Wass, 1996). The differences between ungrazed and grazed treatments represent the net effects of these processes on plant standing crop. I address how such net effects vary with increasing waterfowl densities.

Differences in the species composition of waterfowl assemblages have been previously overlooked in assessments of the effects of waterfowl on plants, with waterfowl analysed typically as a homogenous group (*e.g.* Lodge *et al.*, 1998; Marklund *et al.*, 2002). Most studies quantify waterfowl densities as the number of individuals within a given area (ind. ha^{-1}). In an analysis of waterfowl reductions of plant standing crop in freshwaters, Marklund *et al.* (2002) reported that some of the greatest reductions were associated with the highest waterfowl numerical densities, but there was no statistically significant relationship between waterfowl numerical density and plant standing crop reduction. However, there is a considerable difference in body mass between the smallest (24 g; ocellated crake *Micropygia schomburgkii* Schomburgk, 1848; Taylor, 1998) and largest (11970 g; trumpeter swan *Cygnus buccinator* Richardson, 1832; Kear, 2005) waterfowl, which affects waterfowl species diet and quantity of vegetation consumed (Goodman &

Fisher, 1962; Baldassarre & Bolen, 2006). Thus, an analysis of waterfowl impacts in which waterfowl density is based on bird biomass (kg ha^{-1}) may be more appropriate. Therefore I tested two predictions; the first prediction (P_1) was that there would be no relationship between the reduction in plant standing crop (%) and the mean number of waterfowl within a given area (ind. ha^{-1}). My second prediction (P_2) was that there would be a significant, positive relationship between the reduction in plant standing crop (%) and the mean biomass of waterfowl within a given area (kg ha^{-1}). In the second part of this study I tested for differences in the impact on standing crop between groups of waterfowl species of different body sizes. Waterfowl species have different rates of consumption due to differences in foraging behaviour and energy requirements (Bruinzeel *et al.* 1997), and thus the quantity of vegetation removed per unit time per individual may differ between groups, being greater for larger waterfowl that have higher rates of consumption. Differences in body size amongst waterfowl groups may also lead to differences in non-consumptive destruction, as larger individuals disturb a greater area. I therefore tested the prediction that heavier waterfowl groups would have a greater impact per individual on plant standing crop (P_3). I addressed the assertion that larger waterfowl species would have higher rates of consumption *per se*, testing the prediction that the rate of food consumption would increase with body mass in waterfowl (P_4). Additionally, both the total plant material, and the proportions of specific tissues, in waterfowl diets vary between species (Baldassarre & Bolen, 2006); thus I tested the predictions that herbivory (the percentage of plant material in the diet) would be greater in heavier waterfowl (P_5), and that the proportions of vegetative tissues (leaves and stems) and seeds in the diet would differ between waterfowl species of different masses (P_6).

2.3 Methods

2.3.1 Study species

Waterfowl exhibit a wide range of diets (Goodman & Fisher, 1962; Baldassarre & Bolen, 2006). This meta-analysis focuses on waterfowl species for which plant material (*i.e.* any plant tissues) was listed in the dietary information in Taylor (1998) and Kear (2005), hereafter termed 'plant-consuming waterfowl'. Within the guild of plant-consuming waterfowl there are six principle feeding groups; Rallidae (rails, coots and allies), Anatini (dabbling ducks), Aythyini (diving ducks), Tadornini (sheldgeese, shelducks and allies), Cygnini (swans), and Anserini (geese). Previous authors have tended to disregard Rallidae (hereafter 'rails') when discussing waterfowl (*e.g.* Baldassarre & Bolen, 2006) due to their distant evolutionary relationship to ducks, geese and swans. However, rails exhibit many broad similarities in diet, foraging behaviour and effects on vegetation with other waterfowl (Marklund *et al.*, 2002) so I include them here.

2.3.2 Waterfowl densities and reductions in plant standing crop

I used published experimental (n = 25) and observational (n = 1) studies in any waterfowl habitats where plant standing crop (g DM m^{-2}) had been measured both where waterfowl were present and absent simultaneously. I limited this meta-analysis to studies where waterfowl counts were made in a defined area over a defined period of time. I analysed both single- and mixed-species assemblages, in terms of both plants and waterfowl. I analysed data from 26 suitable studies (**Appendix 1**), from which I calculated two measures of waterfowl density:

$$WID = \text{Waterfowl Individual Density (ind. ha}^{-1}) = \sum_i N_i$$

$$WBD = \text{Waterfowl Biomass Density (kg ha}^{-1}) = \sum_i N_i M_i$$

where N_i = mean population size of waterfowl species i present per hectare during the study period, and M_i = mean body mass (kg) of individuals of species i (as given in Taylor (1998) and Kear (2005)) and the summation is over all plant-consuming waterfowl species. Where sex-related differences in mass were reported, I took the mean values of the male and female body masses. I assumed that all individuals were adults, unless the study indicated the presence of juveniles, in which case body mass values for the appropriate age were used to calculate biomass.

Waterfowl intake rates typically scale with body mass between 0.7-0.8 (Bruinzeel *et al*., 1997; van Gils *et al*., 2007). However, given that herbivore impact on plants does not represent consumption alone (Mitchell & Wass, 1996), and that the allometric scaling of non-consumptive factors is unknown, I assumed a mass exponent of 1.0 in the conversion of *WID* to *WBD* as a conservative approximation. Percentage reduction in plant above-ground standing crop (R) was calculated after Lodge *et al.* (1998) and Marklund *et al.* (2002) as $R = [(B_{\text{-herbivore}} - B_{\text{+herbivore}})/B_{\text{-herbivore}}] \cdot 100$, where $B_{+herbivore}$ and $B_{-herbivore}$ are plant standing crop with and without waterfowl herbivores present respectively. I compared values of plant standing crop at the time of peak standing crop. The use of post-peak values, when the plant is either in recession or dormant, risked confounding decreases in plant standing crop due to herbivory with seasonal recession. Where studies contained multiple values of R which were not statistically independent, for

example multiple values for the same lake, or between-year replicates, I used average values for *R* and waterfowl density.

2.3.3 Differences between waterfowl taxa: implications of body mass

To examine whether reductions in standing crop varied between different taxonomic groups of waterfowl, I analysed the *R* values given in the previous section (**2.3.2**), and calculated a *per capita* reduction in plant biomass (R_s) standardised between different waterfowl densities, using the formula:

$$R_s = R / [P / A]$$

where *P* is the total number of birds present in the study area, and *A* is the study area (in hectares). Estimates of R_s were derived from published studies for flocks of rails (*Fulica spp.* only; $n = 6$ studies), swans ($n = 5$), and geese ($n = 6$). However, no studies of single-species flocks for sheldgeese or ducks could be found that reported the information required to calculate R_s.

2.3.4 Waterfowl size and rates of food consumption

To test whether waterfowl intake rate, and thus the removal rate of plant tissues, increases with body size I analysed 12 published values for waterfowl foraging on terrestrial pasture grasses (*Poaceae*). Selecting *Poaceae*, the plant taxon for which waterfowl intake rates have been quantified most often, allowed me to exclude the confounding effects of plant morphology on intake rate in the analysis. Intake rate is limited by food density below a threshold (*e.g.* Owen, 1972; van Gils *et al.*, 2007).Therefore calculating a mean intake rate averaged over all of the food densities tested in a study would have yielded a value biased by both which, and how many, food densities had been tested. Thus I used the maximum intake rate reported in each study to minimise the confounding effect of food density-limitation on intake rate.

2.3.5 Waterfowl size and herbivorous diet

Two aspects of waterfowl diet composition may affect the magnitude of impacts on plants: the proportion of vegetation (*i.e.* any plant tissue) in the diet and the proportions of different plant tissues consumed. To examine differences in the proportion of diet

comprised by vegetation, I analysed 89 published dietary values (**Appendix 2**) for 56 of the species that consume vegetation according to Taylor (1998) and Kear (2005). Where studies sampled in different seasons I calculated mean values and where multiple studies existed for a single species I calculated mean values for that species. I further analysed the diet data by comparing the percentage of dry weight plant material consumed by each waterfowl group that is comprised of seeds and vegetative material (stems and leaves). Other plant tissues were excluded from this analysis due to lack of sufficient data.

2.3.6 Statistical analyses

I used linear regression analyses to test the relationship between waterfowl density and reductions in plant standing crop (P_1 and P_2). Both sets of estimates of waterfowl density (ind. ha^{-1} and kg ha^{-1}) were log_{10}-transformed to achieve linearity of relationship and normal distribution of residuals. Linear regression analysis was also used to test the relationship between body mass and maximum intake rate of waterfowl species (P_4). I used one-way analysis of variance (ANOVA) to test for differences between waterfowl taxa in (i) impact on plant standing crop (P_3), (ii) percentage of plant matter in diet (P_5), and (iii) percentages of seeds or vegetative tissues in diet (P_6). Statistical analyses were carried out using SPSS version 18 (IBM, US) , with a statistically significant result attributed where $p < 0.05$. Normality of the residuals was confirmed for all data.

2.4 Results

2.4.1 Waterfowl densities and reductions in plant standing crop

I found no relationship between *WID* and *R* ($F_{1,24} = 1.51$, $p = 0.2315$, $R^2_{adj} = 2.0$ %) (**Figure 2.1a**), supporting my first prediction (P_1). However, I found a significant, positive relationship between *WBD* and *R* ($F_{1,24} = 12.77$, $p = 0.0015$, $R^2_{adj} = 32.0$ %) (**Figure 2.1b**), described by the regression equation (coefficient s.e. in brackets):

$$R = 28.24\ (\pm\ 6.00) + 23.88\ (\pm\ 6.68) \cdot \mathrm{Log}_{10}WBD$$

Thus the results support my second prediction (P_2).

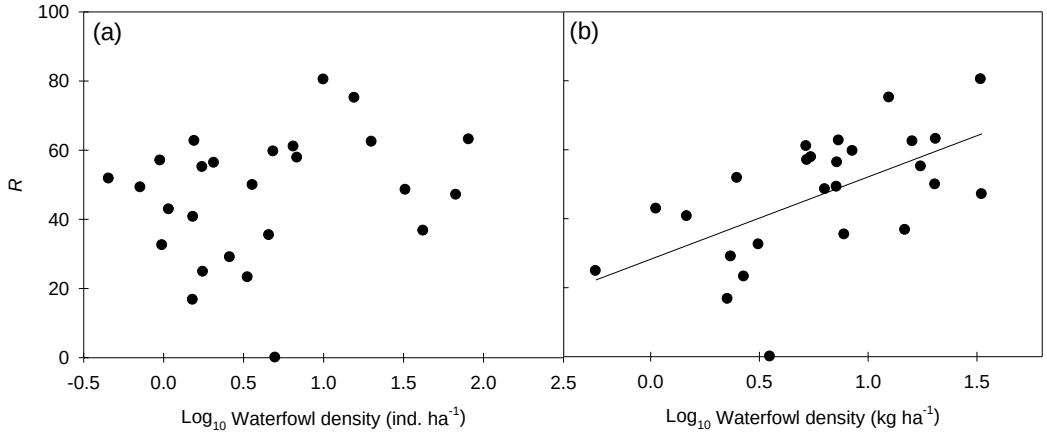


Figure 2.1: *The relationships between reductions in plant standing crop (R) and waterfowl density, estimated as (a) individuals ha^{-1} and (b) kg ha^{-1}, based on data from published studies.*

2.4.2 Differences between waterfowl taxa: implications of body mass

A one-way ANOVA indicated that R_s differed significantly between waterfowl groups ($F_{2,14}$ = 13.81, p < 0.001); *post-hoc* Tukey's tests indicated that swan R_s values were significantly greater than those of geese (p = 0.002) and rails (p = 0.001), but no other comparisons were significantly different (**Figure 2.2**). Thus, these results give partial support to my third prediction (P_3), as differences in impact on plant standing crop were observed between the largest and smallest waterfowl groups, but not between all groups.

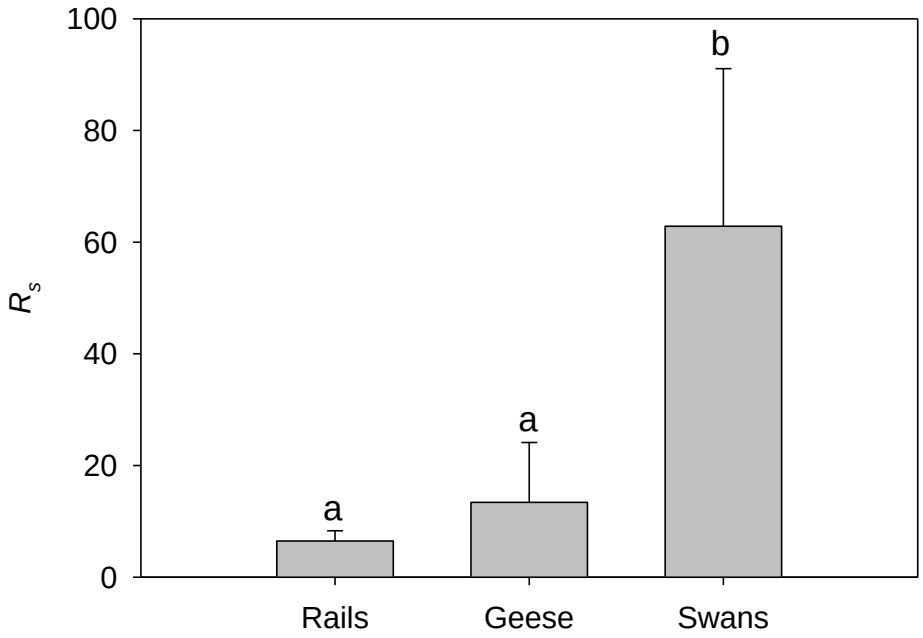


Figure 2.2: *Mean (± 95 % CI) proportional reductions in plant standing crop per individual per hectare (R_s), based on the published values given in Figure 2.1. Different letters indicate significant post-hoc differences between groups.*

2.4.3 Waterfowl size and rates of food consumption

There was a significant, positive relationship between species $\log_{10}$-transformed maximum intake rate I_{max} (g DM s^{-1}) and species $\log_{10}$-transformed body size M (g) ($F_{1,10}$ = 28.75, p = 0.0003, R^2_{adj} = 71.6 %) (**Figure 2.3**), described by the regression equation (coefficient s.e. in brackets):

$$I_{max} = -4.89\ (\pm\ 0.50) + (0.81\ (\pm\ 0.15) \cdot M)$$

These results support my fourth prediction (P_4); a larger species will typically consume vegetation at a faster rate than a smaller species, and thus may have a greater *per capita* impact on plant standing crop per unit time.

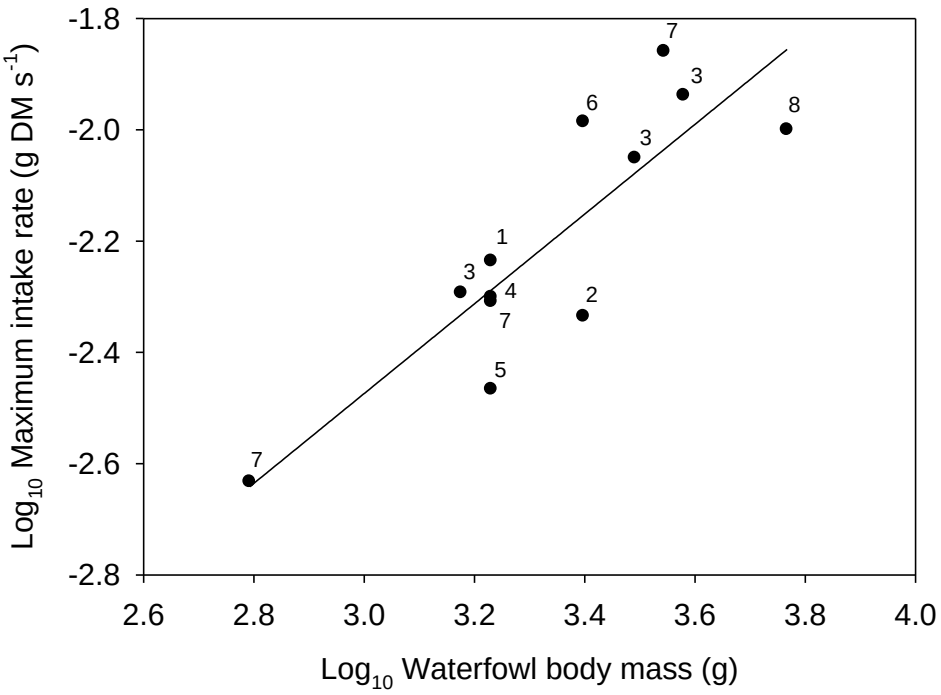


Figure 2.3: *Relationship between log_{10}-transformed waterfowl body mass and log_{10}-transformed maximum dry mass intake rate (I_{max}) on terrestrial pasture grasses. Data from (1) Ebbinge et al., 1975 (barnacle goose); (2) Owen, 1972 (white-fronted goose); (3) Summers & Grieve, 1982 (ruddy-headed goose, upland goose); (4) Prop et al., 1998 (barnacle goose); (5) van der Wal et al., 1998 (barnacle goose); (6) Therkildsen & Madsen, 2000 (pink-footed goose); (7) Durant et al., 2003 (Eurasian wigeon, greylag goose, barnacle goose); (8) van Gils et al., 2007 (Bewick's swan).*

2.4.4 Waterfowl size and herbivorous diet

The proportion of vegetation in diet was significantly different between the six waterfowl groups ($F_{5,55}$= 6.62, p < 0.001). A *Post-hoc* Tukey's test indicated that the percentage of vegetation in diet were significantly lower in diving ducks compared to dabbling ducks (p = 0.007), sheldgeese (p < 0.001), swans (p = 0.001) and geese (p = 0.047), but no other comparisons were significantly different (**Figure 2.4a**). These results offer partial support for my prediction (P_5) that heavier waterfowl are more herbivorous. The proportion of seeds of total plant material consumed in the diet was significantly different between waterfowl groups ($F_{5,23}$ = 5.94, p = 0.001). A *Post-hoc* Tukey's test indicated that seed consumption was significantly higher in dabbling ducks relative to swans (p = 0.009) and geese (p = 0.002) (**Figure 2.4b**). The proportion of stems and leaves of total plant material consumed in the diet was significantly different between waterfowl groups ($F_{5,23}$ = 7.91, p < 0.001). A *Post-hoc* Tukey's test indicated that consumption of stems and leaves was significantly higher in swans relative to dabbling ducks (p = 0.003), diving

ducks (p = 0.007) and rails (p = 0.014), and significantly higher in geese relative to dabbling ducks (p = 0.002), diving ducks (p = 0.007) and rails (p = 0.022), but no other comparison was significantly different. These results offer partial support for my prediction (P_6) that waterfowl mass would affect the proportions of different plant tissues in diet.

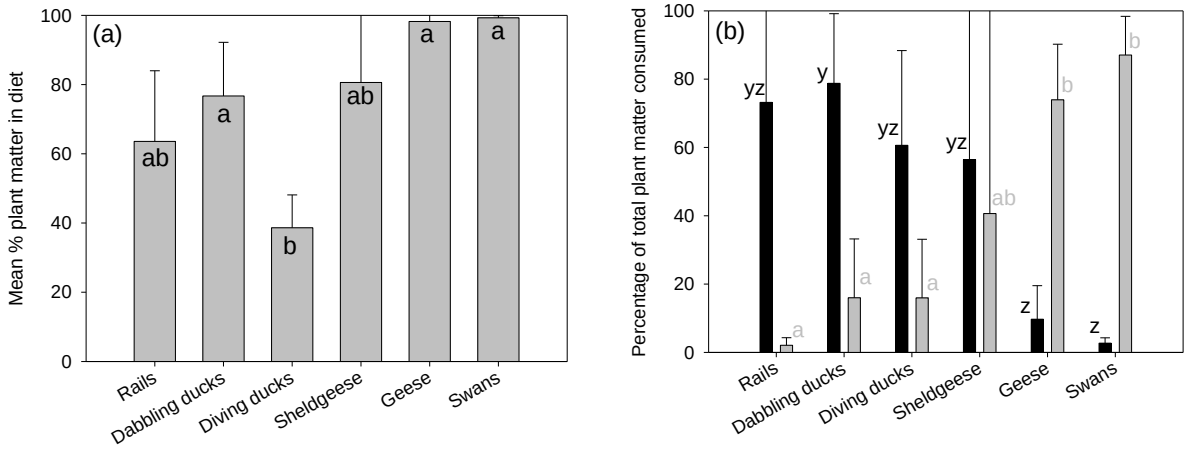


Figure 2.4: *A meta-analysis of (a) the mean (± 95 % CI) percentage of all plant tissues in the diets of 53 species from 89 published values (see supplementary information), based on dry weight, and (b) the mean percentages (± 95 % CI) of herbivorous diets comprised of seeds (dark bars) and vegetative tissues such as leaves and stems (light bars), based on dry weight. Different letters indicate significant post-hoc differences between groups.*

2.5 Discussion

From my meta-analysis of waterfowl impacts on reductions in plant standing crop I present the first demonstration of a significant linear relationship between reductions in plant standing crop and waterfowl biomass density. This relationship enables practitioners to estimate the likely impact on plant standing crop of both natural and managed changes to waterfowl populations. That reductions in plant standing crop were related to waterfowl density estimated as kg ha^{-1}, but not waterfowl density estimated as ind. ha^{-1}, suggests that it is the biomass of waterfowl rather than the number of individuals which is the more important determinant of waterfowl effects on plant standing crop (Gyimesi *et al*., 2011). The largest reductions in plant standing crop should thus be observed at sites where high-densities of large-bodied waterfowl congregate, such as

annual moult sites and other areas where large non-breeding flocks gather to feed (Kear, 2005; Baldassarre & Bolen, 2006). Currently, most studies of waterfowl herbivory analyse the impacts on plant standing crop based on the number of waterfowl present, regardless of species. Greater recognition amongst waterfowl biologists is therefore needed of the importance of body mass when determining waterfowl impacts on plant standing crop. However, the relationship with biomass should be used cautiously as the spread of data around the mean regression line is considerable. Future research could incorporate factors other than waterfowl density that may influence waterfowl impacts on plant standing crop, such as plant life-history (*e.g.* growth rate, age, competitiveness, anti-herbivore defences) and environmental factors (*e.g.* water depth, light, temperature, CO_2 availability; Bornette & Puijalon, 2011; Gayet *et al*., 2011b). Intraspecific differences in body mass also exist, for example between sexes and between age classes; whether intraspecific differences in body mass also affect reductions in plant standing crop should be investigated further.

Swans had significantly higher *per capita* impacts on plant standing crop relative to geese and rails, probably due to the greater body mass and associated greater energy requirement, intake rate, and proportion of plant tissues in the diet. I was unable to estimate the *per capita* impacts on plant standing crop of sheldgeese, dabbling ducks, or diving ducks as there were no published single-taxon studies of these groups. Future studies could quantify the *per capita* impacts of these groups and compare the values to those presented in this study for swans, geese, and rails. Such *per capita* impacts are difficult to measure in wild waterfowl populations as individuals often live in mixed-taxon flocks (Baldassarre & Bolen, 2006). The impacts of small duck species could be assessed with the use of fencing that excludes larger-bodied waterfowl from the study area (*e.g.* Badzinski *et al*., 2006). Alternatively, *per capita* impacts on plant standing crop could be measured for a species or taxon (a flock of individuals of different species but the same group, *i.e.* dabbling ducks) under controlled *ex situ* conditions such as artificial pools in a laboratory.

Large waterfowl (> 2500 g) are almost exclusively vegetarian, whilst smaller species exhibit a range of diets from omnivory to exclusive herbivory. Bruinzeel *et al.* (1997) analysed waterfowl allometry and found that waterfowl energy intake rate scales with a power of body mass of between 0.78 and 0.85, whereas daily energy expenditure scales with the power 0.68. In this study I found that maximum intake rate scaled with a power of body mass of 0.81. Thus small waterfowl such as dabbling ducks must devote more time to foraging than larger waterfowl, or seek food of higher nutritional quality (Demment & van Soest, 1985). Vegetation is typically low in nitrogen and high in fibre relative to

animal tissue (Baldassarre & Bolen, 2006). My results suggest that smaller waterfowl rely less on lower quality vegetation and more on higher quality animal matter. Thus an individual of a small species will consume a lower quantity of vegetation, due to both a lower total energy requirement and a lower proportion of vegetation in their diet, than an individual of a larger species. As leaves and stems comprise a greater proportion of plant standing crop relative to seeds (Grime, 2002), consumption of the former will likely have a greater impact on plant standing crop than consumption of the latter, at least in the short term (Maron & Gardner, 2000).

How reductions in plant standing crop affect the abundance and behaviour of other organisms is currently poorly understood. There is a particular need to study the potential impacts on organisms with ecological and economic importance, such as fish. Several studies have demonstrated that populations of birds, small mammals, and invertebrates have been reduced due to waterfowl herbivory (*e.g.* Sammler *et al.*, 2008; Samelius & Alisauskas, 2009), but whether these reductions are typical or exceptional requires further investigation. The mechanisms by which vegetation losses caused by waterfowl herbivory alter animal abundances are unclear. Several mechanisms have been proposed, including loss of refugia, reduced food availability, and physical disturbance caused by grazing. Future experiments that demonstrate the relative importance of these and other mechanisms are needed.

The ability to predict the effects of waterfowl on plant standing crop would aid management and conservation of both taxa and their associated habitats. Ecological modelling represents a potential tool for predicting the consequences of waterfowl foraging on plants. Resource-consumer models, such as individual-based models (IBMs), can generate predictions of plant biomass depletion, waterfowl foraging effort, waterfowl distribution, and habitat carrying capacity, from data on waterfowl energy requirements, food intake rates, plant distributions, and plant energy content and digestibility (Grimm & Railsback, 2005; Stillman & Goss-Custard, 2010; **Chapter 8**). Such predictions allow the spatiotemporal patterns of plant depletion to be quantified and strategies for both herbivore and plant management to be tested.

Chapter 3: Measuring submerged macrophyte standing crop in shallow rivers: a test of methodology.

3.1 Abstract

High natural variability in space and time can make accurate measurements of macrophyte standing crop difficult. The accuracy of such measurements could be improved by quantifying the relationships between the different methods of measuring standing crop which are available to researchers. In this study I compare cover, volume, and biomass as measures of standing crop. Percentage cover, percentage volume, and dry weight biomass estimates were positively related ($R^2_{(adj)}$ range = 54 – 96 %), but these relationships were significantly different between sites, and to a lesser extent between months. Biomass was related ($R^2_{(adj)}$ range = 18 – 73 %) to stand height. Furthermore, cover, volume and biomass indicated different seasonal trends in standing crop at the two study sites. This study presents a suite of standing crop measures that exhibit close congruence, can be measured efficiently and minimise destructive sampling *in situ*, attributes which will aid in the design and implementation of future macrophyte measurement protocols for shallow rivers.

3.2 Introduction

A wide range of studies have documented the important roles macrophytes play in the structure and functioning of aquatic ecosystems (*i.e.* Landers, 1982; Carpenter & Lodge, 1986; Cotton *et al*., 2006). Quantitative assessments of these roles require accurate measurements of standing crop (*i.e.* abundance). However, plant standing crop varies in both space and time, and measurements can be costly in terms of time and effort, highlighting the need to develop efficient sampling methods (Downing & Anderson, 1985; Spears *et al*., 2009; Gunn *et al*., 2010). The three most commonly used measures of standing crop are (a) cover (%), the proportion of a given benthic area occupied by macrophytes, (b) volume occupied (%), the proportion of a given volume of water occupied by macrophytes, and (c) biomass (g m^{-2}), the mass of plant material in a given area or volume (Murphy, 1990; Gunn *et al*., 2010). Traditional methods of biomass estimation are destructive (*e.g.* Hiley *et al*., 1981; O'Hare *et al*., 2010a; Johnson & Newman, 2011), which in many instances is not desirable; for example, when removal of biomass interferes with subsequent observations, in studies of protected species, or in the study of animals associated with macrophytes where removal of biomass may alter the behaviour or abundance of the study animal (Gouraud *et al*., 2008; **Chapter 2**; **Chapter 8**). There is therefore a need to develop and test methods that either remove or

translocate the destruction outside the area of interest, whilst retaining the ability to accurately estimate biomass. Alternatively, the ability to use cover or volume as a robust surrogate for biomass would remove the need for destructive biomass sampling.

Whilst cover, biomass and volume have been used interchangeably as measures of standing crop, they may not concur as each represents a different aspect of the macrophyte stand. There is some limited evidence to suggest a positive relationship between cover and biomass (Dawson, 1978; O'Hare *et al*., 2010b; Yin & Kreiling, 2011). However, due to the spatiotemporal variability of plant stand structure, the strength of such relationships may not be constant across space and time (Downing & Anderson, 1985). Given the importance of accurate estimates of plant standing crop for conservation, hydrological and environmental management purposes, there is a need to (i) quantify the relationships between the cover, volume and biomass of aquatic plant stands, and (i) determine how such relationships vary in space and time.

This study tested two hypotheses regarding the relationships between plant cover, biomass and volume. The first hypothesis was that these three measures of plant standing crop would be positively related. The second hypothesis was that these relationships would vary in space (*i.e.* between sites) and time (*i.e.* between months).

3.3 Methods

3.3.1 Study sites

This study was conducted between March and September 2009, covering the macrophyte growth cycle from growth to recession (Ham *et al*., 1981; Flynn *et al*., 2002; Cotton *et al*., 2006), at two sites on a mesotrophic chalk river, the River Frome (Dorset, UK); a headwater site at Maiden Newton and a mid-reaches site at East Stoke (**Table 3.1**). Detailed site information can be found in Wharton et al. (2006).

The River Frome macrophyte assemblage is almost exclusively dominated by water crowfoot (*Ranunculus penicillatus ssp. pseudofluitans* (Syne) S.D. Webster), with *Potamogeton spp.*, *Elodea canadensis* Michx., *Zannichellia palustris* L., *Sparganium emersum* Rehmann, *Oenanthe fluviatilis* (Bab.) Coleman, *Nasturtium officinale* W.T. Aiton, and *Myriophyllum spicatum* L., also present in low abundance at East Stoke (Cotton *et al*., 2006; Wharton *et al*., 2006; O'Hare *et al*., 2007).

Table 3.1: *Characteristics of the two River Frome study sites over the March – September study period.* [a] *data (1998-2003) from Wharton* et al*. (2006).*

	Maiden Newton	**East Stoke**
Latitude, Longitude	50°46'N, 02°34'W	50°41'N, 02°11'W
Length of study reach (m)	10.0	10.0
Mean channel width (m)	5.1	15.5
Mean depth (m)	0.33	0.45
Area of study reach (m^2)	51.0	155.0
Riparian shading (%)	10	0
Mean Q (m^3 s^{-1})	0.6[a]	5.5[a]
Peak Q (m^3 s^{-1})	1.6[a]	24.0[a]

3.3.2 Measuring macrophyte cover, volume, and stand height

At each site a 10 m-long reach, characteristic of that site, was selected from which measurements were made in March, May, July and September. Before any in-stream measurements were made, macrophyte cover was estimated visually from the bank-side in 5 % increments at the upstream limit of the reach. For the in-stream estimates of cover, I began at the bottom of the 10 m reach and walked upstream. At 1 m intervals, transects were measured across the entire width of river, with a 0.5 x 0.5 m quadrat laid end-on-end. For each quadrat, the percentage cover of each macrophyte species was estimated in 5 % increments. Depth was measured at the quadrat centre to the nearest 0.05 m and the quadrat volume (m^3) was calculated as the quadrat area (0.25 m^2) multiplied by depth (m). If a macrophyte stand was present within the quadrat, depths to the top and bottom of the plant nearest to the centre of the quadrat were measured to the nearest 0.05 m. Macrophyte stand height (m) was given by subtracting these depths from total depth. Macrophyte volume (m^3) was calculated from the area covered by macrophytes (m^2) multiplied by the stand height (m). The percentage of quadrat volume occupied by macrophytes was calculated as:

(macrophyte volume / quadrat volume) · 100

The same quadrats were measured in March, May, July and September.

3.3.3 Estimating biomass from stand height

Biomass samples were taken with a 0.00785 m^2 hand corer immediately downstream of each 10 m reach where cover and volume had been measured. Thirty samples were taken each month at different downstream locations on each sampling occasion to preclude the effects of previous biomass removal, but all samples were taken within 40 m of the original study reach, in reaches with similar morphological and habitat characteristics. Samples were taken at each site in March, May, July and September, each from a different water crowfoot plant. Water crowfoot was selected as it dominates the chalk river macrophyte assemblage and the study reaches (Dawson, 1976a; Flynn *et al*., 2002). Before each sample was taken the water depth, and depths to the top and bottom of the plant were recorded (± 0.05 m). The sampler then placed their hand underneath the plant stand and lowered the corer onto the hand, trapping part of the stand in the corer (Westlake *et al*., 1986). The plant material outside of the corer was then trimmed off and the sample labelled. In the laboratory non- water crowfoot material was carefully removed and the water crowfoot sample dried to constant weight at 60 ˚C using a Heraeus Kelvitron T oven (Thermo Fisher Scientific, Loughborough, UK). Dry mass (DM) was measured to within ± 0.01 g on a Sartorius PT120 balance (Sartorius GMBH, Germany).

3.3.4 Statistical analyses

All statistical analyses were carried out using SPSS version 18 (IBM, US), with a statistically significant result attributed where $p < 0.05$. Normality of the regression and model residuals was confirmed for all data. To examine the consistency between sites and between months of the relationship between the values per quadrat for percentage cover (*C*),volume occupied (*V*), and dry mass biomass (*B*) I tested mixed effect repeated measures models (using SPSS routine MIXED) of (i) cover (%) with volume (%) as a covariate, (ii) cover (%) with biomass (g DM m^{-2}) as a covariate, and (iii) volume (%) with biomass (g DM m^{-2}) as a covariate; in each model, site and month were fixed factors and sampling quadrat within site was treated as a random factor subject to repeated measurement (March, May, July, September) with auto-regressive AR(1) auto-correlations between successive sampling months. For each site-month combination a linear regression analysis was used to assess the relationship between the three measures of standing crop. Linear regression was also used to compare percentage cover estimated visually from the riverbank and mean measured cover values using in-stream quadrats for each reach for all months. To examine the consistency between sites and between months of the relationship between the biomass and height of macrophyte stands I tested a univariate GLM of $\log_{10}$-transformed R_{CI} (range of the confidence intervals) with $\log_{10}$-transformed sample size as a covariate and site and month as fixed factors. As different macrophyte stands were sampled on each occasion, a repeated

measures analysis was not appropriate here. To calculate the biomass per reach per month at each site, the height-mass regression relationship derived downstream of the reach was applied to the measured stand height values within the reach to give the mass per hypothetical core for each quadrat. This value was divided by the core area (0.00785 m^2) and then multiplied by the area covered by macrophytes in that quadrat (m^2) to yield the biomass. As the quadrat area was 0.25 m^2, the biomass per square metre for each quadrat was calculated by multiplying the quadrat biomass by 4. Total biomass per 10 m reach was calculated as the average biomass per quadrat (m^{-2}) multiplied by the reach area (m^2).

3.4 Results

3.4.1 Cover, volume, and biomass measures

At Maiden Newton, macrophyte percentage cover increased from March to a maximum in July and decreased thereafter, whilst at East Stoke cover increased consistently from March to September (**Figure 3.1a**). Small-scale variation (*i.e.* between 0.25 m^2 quadrats) was high in all months at each site (**Figure 3.2**). The macrophyte assemblage was dominated by water crowfoot in all months, comprising a mean (± 95 % CI) of 99 ± 1 % of the total macrophyte cover at Maiden Newton and 92 ± 3 % at East Stoke. The remainder of plant cover was comprised of limited quantities of *Potamogeton spp.*, *E. canadensis*, *Z. palustris*, *S. emersum*, *Oenanthe spp.*, *N. officinale*, and *M. spicatum* at East Stoke, and *Oenanthe spp.* at Maiden Newton.

Table 3.2: *Mixed model significance test p value for each factor (Site, Month and Covariate) and their interactions, together with the estimation temporal auto-correlation (AR(1)) of the repeat bi-monthly measurements on each sample quadrat of each site.*

Mixed Model term	**Y variable ~ Covariate**		
-	Cover ~Volume	Cover ~ Biomass	Volume ~ Biomass
Site	0.386	0.725	0.003
Month	<0.001	<0.001	0.108
Site x Month	<0.001	<0.001	0.336
Covariate	<0.001	<0.001	<0.001
Site x Covariate	<0.001	<0.001	0.003
Month x Covariate	<0.001	<0.001	<0.001
Site x Month x Covariate	<0.001	<0.001	<0.001
Auto-Correlation AR(1)	0.043	0.083	0.174

At Maiden Newton, percentage volume occupied by macrophytes (mean ± 95 % confidence interval) followed a similar increase from March as cover (13.6 ± 1.2 %, *n* = 102) but peaked sooner in May (34.2 ± 6.4 %, *n* = 104) before decreasing thereafter. At East Stoke, volume mirrored the patterns observed for cover by increasing consistently from March (6.9 %, ± 1.2 %, *n* = 309) to September (22.1 % ± 2.1 %, *n* = 302) (**Figure 3.1c**). In the mixed effects repeated measures models allowing for the potential of interaction between both site and month with the slope of the relationship with the covariate, all interactions with covariate slope were statistically significant for the cover versus volume, cover versus biomass and volume versus biomass relationships (**Table 3.2**). Thus I carried out linear regression analyses between cover, volume, and biomass for each site-month combination; cover, volume, and biomass were strongly, positively related in all months at both sites (**Table 3.3**). A significant relationship was also detected between in-stream and bank-side estimates of cover ($F_{1,6}$ = 12.01, p = 0.0132, $R^2_{(adj)}$ = 61.3 %; **Figure 3.3**), over the range of measured cover values tested (24.9 – 68.2 %).

3.4.2 Biomass measures and estimates from stand height

Macrophyte biomass (mean ± 95 % confidence interval) at Maiden Newton increased from 161.7 ± 50.1 g DM m^{-2} (*n* = 102) in March to 398.4 ± 74.5 g DM m^{-2} (*n* = 91) in July, before declining to 169.4 ± 49.8 g DM m^{-2} (*n* = 94) in September, while at East Stoke biomass increased from 74.0 ± 12.2 g DM m^{-2} (*n* = 309) in March to 222.9 ± 22.5 g DM m^{-2} (*n* = 302) in September (**Figure 3.1b**). However, the East Stoke reach had a consistently greater total dry Wt biomass per 10 m reach due to the greater river width (15.5 m versus 5.1 m; **Table 3.1**); total biomass per 10 m reach at Maiden Newton increased from 8246.9 g DM in March to 20318.4 g DM in July, before declining to 8641.0 g DM in September. At East Stoke total reach biomass increased consistently from 11465.5 g DM in March to 34550.9 g DM in September. A GLM of macrophyte biomass-stand height relationships indicated that a model in which intercept and slope were dependent on both site and month best explained the variance in biomass ($F_{9,230}$ = 46.039, p < 0.001, $R^2_{(adj)}$ = 62.9 %). Therefore site- and month-specific height-mass equations were used to calculate biomass in the 10 m reaches (**Table 3.4**).

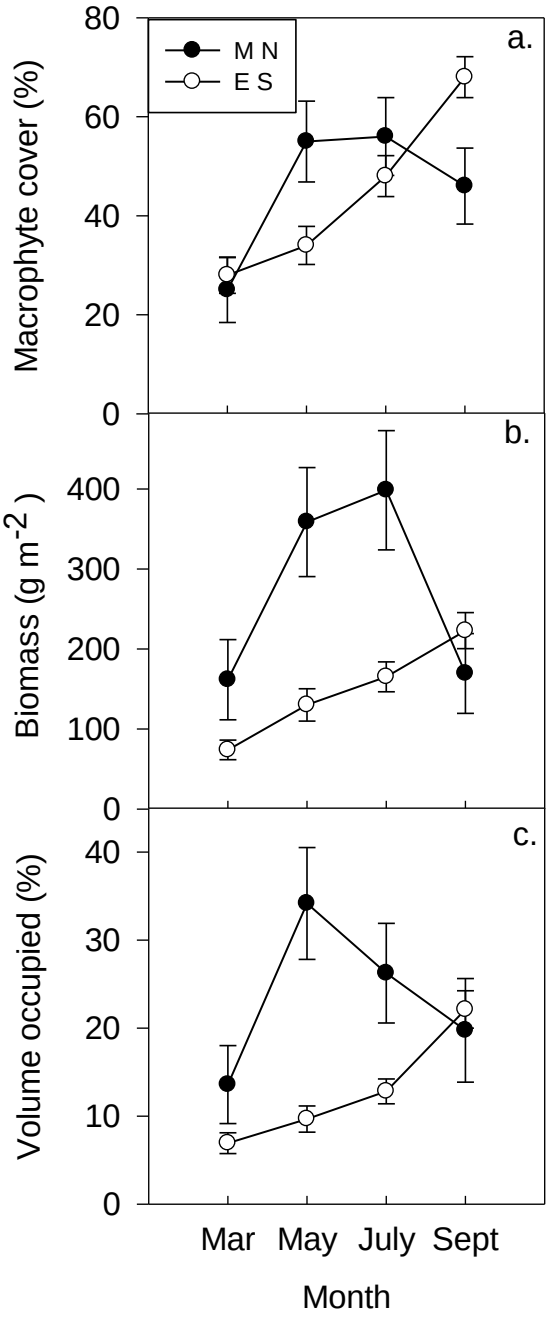


Figure 3.1: *Seasonal changes in mean (± 95 % confidence intervals) macrophyte cover (a), dry mass biomass (b), and volume (c) at Maiden Newton (MN) and East Stoke (ES).*

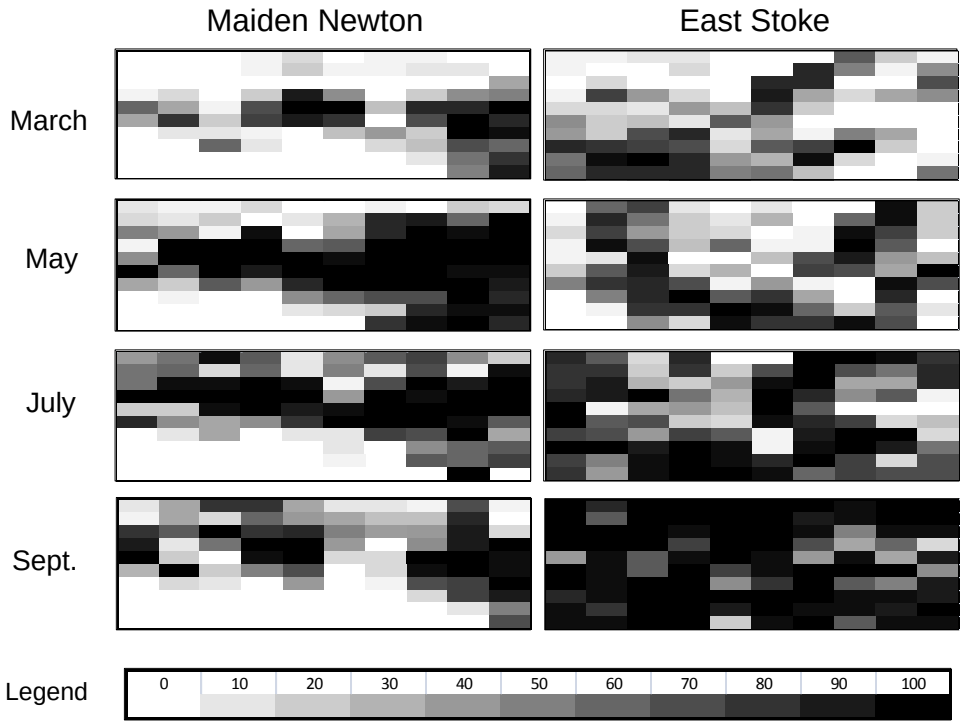


Figure 3.2: *Block diagrams indicating the variability in percentage macrophyte cover in 0.5 x 0.5 m quadrats in a 10 x 5 m section of river at the two sites. The river flowed right to left.*

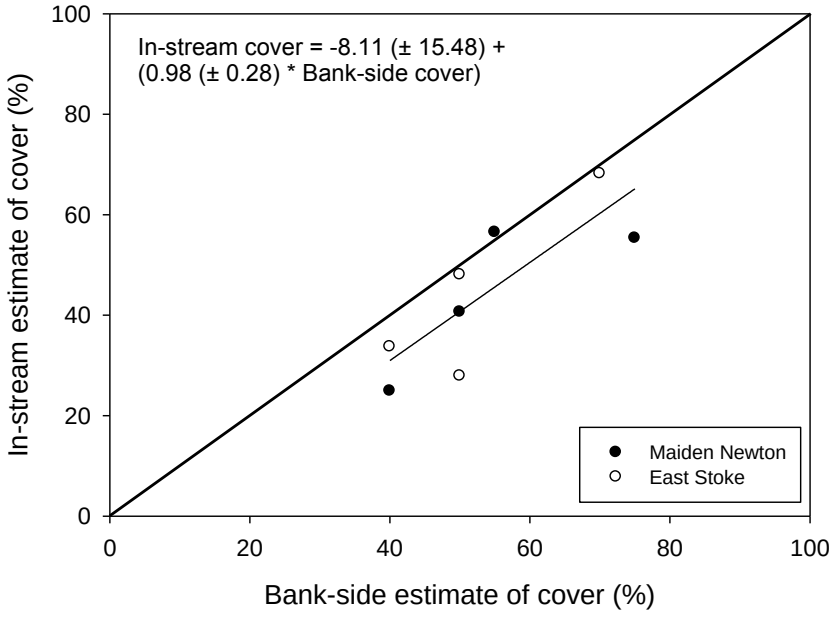


Figure 3.3: *The linear relationship (± SE) between in-stream and bank-side estimates of percentage macrophyte cover, based on mean data for all sites and months. A 1:1 line is included for comparison.*

Table 3.3: *The results of the linear regression relationships between macrophyte cover (%), percentage volume occupied (%), and biomass (g DM m^{-2}) for each month at the two sites. All relationships were significant ($p < 0.0001$).*

Comparison	Site	Month	Intercept (± SE)	Slope (± SE)	d.f.	$R^2_{(adj)}$
Cover-Volume	Maiden Newton	March	6.47 ± 1.53	1.36 ± 0.06	101	85 %
		May	17.03 ± 2.94	1.12 ± 0.06	103	76 %
		July	28.17 ± 3.52	1.08 ± 0.09	90	60 %
		Sept.	19.10 ± 2.63	1.09 ± 0.07	93	69 %
	East Stoke	March	9.48 ± 1.12	2.66 ± 0.09	308	75 %
		May	12.62 ± 1.29	2.18 ± 0.08	314	71 %
		July	14.49 ± 1.37	2.62 ± 0.08	318	79 %
		Sept.	35.10 ± 2.09	1.50 ± 0.07	301	59 %
Cover-Biomass	Maiden Newton	March	-12.33±13.13	6.99 ± 0.31	101	83 %
		May	-5.48 ± 8.16	1.72 ± 0.12	103	68 %
		July	-54.65 ± 36.53	8.02 ± 0.54	90	71 %
		Sept.	-42.00 ± 22.35	5.20 ± 0.40	93	64 %
	East Stoke	March	-6.88 ± 4.05	2.90 ± 0.09	308	75 %
		May	-15.32 ± 8.27	4.32 ± 0.17	314	67 %
		July	-19.38 ± 8.09	3.84 ± 0.13	318	73 %
		Sept.	-50.57 ± 16.42	4.01 ± 0.21	301	54 %
Volume-Biomass	Maiden Newton	March	22.25 ± 12.53	10.27 ± 0.47	101	82 %
		May	8.40 ± 5.80	2.38 ± 0.12	103	79 %
		July	114.82 ± 30.29	10.80 ± 0.80	90	67 %
		Sept.	25.60 ± 15.75	7.28 ± 0.45	93	74 %
	East Stoke	March	4.33 ± 1.52	10.06 ± 0.12	308	96 %
		May	3.79 ± 3.52	13.08 ± 0.21	314	92 %
		July	1.77 ± 3.79	12.76 ± 0.21	318	92 %
		Sept.	-1.00 ± 5.26	10.13 ± 0.18	301	91 %

Table 3.4: *The results of the linear regression relationships between biomass per core (g DM) and macrophyte stand height (m) for each month the two sites. All relationships were significant (p < 0.01).*

Site	Month	Intercept (± SE)	Slope (± SE)	d.f.	$R^2_{(adj)}$
Maiden Newton	March	0.93 ± 0.56	21.20 ± 3.55	29	54
	May	1.21 ± 0.54	20.64 ± 3.09	29	60
	July	-1.66 ± 1.28	60.61 ± 9.69	29	57
	Sept.	0.83 ± 0.70	25.53 ± 4.37	29	53
East Stoke	March	-0.42 ± 0.25	22.65 ± 2.53	29	73
	May	1.97 ± 0.48	11.91 ± 4.39	29	18
	July	-0.09 ± 0.45	25.93 ± 5.09	29	46
	Sept.	0.28 ± 0.47	14.44 ± 2.35	29	56

3.5 Discussion

In this study I have quantified the relationships between the three most commonly-used measures of plant standing crop; cover, volume and biomass. I am not aware of any previous study that has examined these three relationships. Strong, positive relationships were detected between all three measures, but such relationships typically varied between site and month. I demonstrated the application of a method of biomass measurement which avoided influencing subsequent macrophyte growth and biomass by relocating destructive sampling downstream of the main study reach. The results of both analyses will facilitate efficient future sampling in shallow rivers.

I estimated values of macrophyte standing crop over a cycle of growth and recession were within the seasonal ranges reported in other studies of the chalk river macrophyte community (Dawson, 1976a; Ham *et al*., 1981; Armitage & Cannan, 2000; Flynn *et al*., 2002). Percentage cover, percentage volume, and dry weight biomass co-varied in accordance with the first hypothesis, concordant with previous studies which had reported positive relationships (O'Hare *et al*., 2010b; Yin & Kreiling, 2011). However, a 1:1 relationship was not found for any relationship. The relationships between cover and biomass or volume are likely to reflect the trade-off between the horizontal and vertical growth of plant stands (Duartes *et al*., 1996). In particular percentage volume values were always lower than percentage cover, probably reflecting the growth form of water crowfoot which often maximises canopy at the water surface (Dawson & Robinson, 1984). Macrophytes such as water crowfoot, which spread at the surface over large areas from rooted stems, will typically have cover values which are high relative to biomass or

volume (Edwards & Brown, 1960). Thus plant morphology and growth form are likely to influence the relationships between cover, biomass and volume. As volume also indicated a slightly different seasonal trend in standing crop than cover or biomass, cross comparisons of data derived by the different methods should be treated cautiously and attention paid to the growth form of the study species. The stems produced by water crowfoot during the flowering phase, April to June, are more buoyant than stems produced at other times of year, which could result in a higher volume per cover/biomass during the flowering phase (Dawson, 1976a). However, I found no evidence that the relationships between volume and cover or biomass became biased towards volume during the flowering phase; thus the increase in stand volume observed in May likely reflected an increase in the quantity of plant material both horizontally and vertically in the water column, hence the observed concomitant increases in cover and biomass. In addition, the relationships between cover, volume and biomass varied in space (*i.e.* between sites) and time (*i.e.* between months) in accordance with the second hypothesis. Such variance may be due, at least in part, to differences in plant morphology; the architectural properties of aquatic plants (*i.e.* leaf size) are known to vary within-species with differences in both season and habitat (Duartes, 1991). Species other than water crowfoot were of minor importance (< 8 % total cover). Thus it is unlikely that spatiotemporal variance in the relatedness of measures of standing crop was influenced by changes in plant community composition or the relative importance of different species with contrasting architectures.

The use of sampling methods that measure biomass indirectly by relocating destruction outside the main study area can facilitate the temporal study of protected species and animals associated with macrophytes where removal of biomass may alter the behaviour or abundance of the study animal (Gouraud *et al*., 2008), where it is critical that the sampling method does not modify the existing biomass or its growth. However, a potential source of error in translocating destructive sampling to a secondary area is that differences in the stand height-biomass relationship may exist between the two areas. Indeed in this study I detected that the stand height-biomass relationship differed between sites, although substantial physical and hydrological differences existed between the sites (**Table 3.1**). Future studies using this method could minimise potential error due to between-site differences by adopting this approach of translocating the destructive sampling over the shortest possible distance. A full validation would test the method against destructive *in situ* sampling in synchrony in the same area. However, destructive sampling is only likely to bias such studies if sampling removes or impacts on the growth of a sufficient quantity of macrophyte material to influence subsequent measures of abundance. In this study the removed material as a proportion of the macrophyte biomass in a reach was negligible; even where macrophyte biomass was lowest (Maiden Newton, March) sampling-related destruction accounted for < 1.4 % of

biomass within a 10 m reach. Wright *et al*. (1981) concluded that repeated monthly sampling of chalk river macrophytes (area = 0.05 m^2, *n* = 25 per month), using a similar method to this study, did not affect subsequent measures of abundance. Therefore, repeated sampling may not affect future macrophyte abundance, when both the sampler size and sample number are small. In plant habitats where these assumptions are met, indirect biomass estimation could provide a useful means of obtaining accurate estimates of biomass without destructively sampling in the immediate areas of interest.

Comparison of cover estimates made in-stream and on the bank-side suggested that visually estimating macrophyte cover from the river bank resulted in an overestimate of cover (127 %) relative to in-stream estimates. Whether the consistent overestimation of cover is an inherent bias in the visual estimate method *per se* or an individual bias is impossible to determine as only one observer was tested in this study. Similarly the low spatial replication (*n* = 2) means that I was unable to test whether overestimation was more likely at sites with certain hydrogeomorphological characteristics. An advantage of visual estimates of cover is that they take much less time than in-stream measurements, and thus reduce required sampling effort and cost. In this study visual estimation took less than one minute at each site, compared with the 120 (Maiden Newton) and 240 (East Stoke) minutes required for in-stream measurements. My results suggest that as a way of measuring macrophyte cover, bank estimates can be a much quicker, if less accurate method than in-stream measurements. My results are reassuring given the widespread use of bank-based cover estimates in routine monitoring programmes, such as the Mean Trophic Rank Methodology which is based on rapidly assessing a 100 m reach (Dawson *et al*., 1999).

The methods demonstrated here provided detailed estimates of the changes in plant standing crop over the seasonal cycle of growth and recession. However, the substantial time and effort required at each site ultimately limits the number of sites for which trends in plant standing crop can be quantified. For example, in this study I was limited to just two sites. A study of herbivore-plant interactions limited to just two study sites would offer little insight due to the lack of spatial replication, thus less time- and effort-intensive methods of estimating plant abundance will be required for the study of swan-plant interactions in this thesis (**Chapter 4**). The use of bank-side estimates of percentage cover, identified in this study, offers one potential method. The use of destructive in-situ biomass sampling (*e.g.* Westlake *et al*., 1986) appears unlikely to impact future growth where the number of required samples is low (Wright *et al*., 1981; this study) and therefore may represent a more efficient method of estimating plant abundance at larger numbers of sites in studies of herbivore-plant interactions.

Chapter 4: Responses of a shallow river plant community to four variables vary across the plant growth cycle.

4.1 Abstract

How plant community responses to biotic and abiotic factors vary over time is poorly understood. In particular, plant community regulation in shallow rivers has received little attention, despite the high abundances and keystone roles of plants in such ecosystems. Understanding plant community responses to combinations of biotic and abiotic factors is critical for predicting ecosystem response to environmental change. I studied an aquatic plant community dominated by water crowfoot (*Ranunculus penicillatus ssp. pseudofluitans*) in an ecosystem subject to gradients in mute swans (*Cygnus olor*) herbivory, riparian shading, water temperature and distance downstream of the river source. I quantified abundance, species richness, evenness, flowering and dominance in relation to biotic and abiotic factors during the growth-, peak-, and recession-phases of the plant growth cycle. The relative importance of biotic and abiotic factors varied between different phases of the plant growth cycle. Herbivory became more important during the later phases of peak abundance and recession due to an influx of swans from adjacent pasture fields. Shading by riparian vegetation also had a greater depressing effect on biomass in later seasons, probably due to increased leaf abundance reducing light intensity reaching the aquatic plants. The effect of temperature on community diversity varied between upstream and downstream sites by altering the relative competitiveness of species at these sites. High swan densities, which reduced plant abundance within a year, did not influence abundance in subsequent years. These results highlight the importance of seasonal patterns in regulation of plant community structure.

4.2 Introduction

Herbivores can have a significant impact on plant communities by reducing plant abundance (Cyr & Pace, 1993; Polis, 1999; **Chapter 2**) and altering plant community composition (Milchunas *et al*., 1988; Milchunas & Lauenroth, 1993; Gross *et al*., 2001). However, herbivory is only one form of disturbance (*sensu* Grime *et al*., 1988), and plants are also subject to stress and productivity gradients (Hilton *et al*., 2006; Kohler *et al.*, 2010). Key factors that regulate plant community structure and function are temperature (Morison & Lawlor, 1999; Bornette & Puijalon, 2011), light availability (Dawson, 1976b; Kohler *et al.*, 2010) and concentrations of growth-limiting nutrients (Spink *et al.*, 1993; Hilton *et al*., 2006). However, an unresolved issue in ecology is how such additive and

interactive biotic and abiotic factors regulate plant community structure and function over time (Huntly, 1991; Polis, 1999).

Our understanding of the relative effects of biotic, in particular herbivory, and abiotic factors on river plant communities is particularly limited. Whilst several studies have tested the relative effects of herbivory and a limited number of other factors simultaneously in shallow lakes (Weisner *et al.*, 1997; Nolet, 2004), temperate woodlands (Louda *et al.*, 1987), and grasslands (Bullock *et al*., 2001; Olofsson, 2001), there have been no such studies of rivers, despite the importance of plants in, and widespread distribution of, river ecosystems. For rangelands and shallow lakes in particular, the interactive impact of herbivory on plant communities is considered as part of wider system function that includes other biotic with abiotic factors (HilleRisLambers *et al*., 2001; Jones & Sayer, 2003; Rietkerk *et al*., 2004; Searle *et al*., 2009). Such an approach has been important in managing ecosystems subject to adverse environmental change, including anthropogenic influence, and the combined impact of biotic and abiotic factors on plant communities has been fundamental to ecosystem response. Evidence from other ecosystems suggest herbivory can alter dominance relationships within plant communities (Gross *et al*., 2001; Sandsten & Klaassen, 2008; Hidding *et al*., 2010). However, for shallow rivers, so little is known about the role of herbivory that current theory on ecosystem function in response to anthropogenic pressure, eutrophication in particular, does not include it (Hilton *et al*., 2006).

One river type that may be strongly affected by herbivory is chalk rivers. Water crowfoot (*Ranunculus penicillatus pseudofluitans* Webster) dominates these communities hence when factors alter its abundance, they may decrease its competitiveness indirectly and thus increase community evenness and richness. Plant communities in chalk rivers are hypothesised to be regulated by mute swan (*Cygnus olor* Gmelin, 1789) herbivory, and gradients of other biotic factors, such as riparian shading, and abiotic factors, such as water temperature and factors associated with distance downstream from the river source such as water depth, sediment type, and discharge (Dawson, 1976a; Dawson, 1980; Dawson *et al*., 1981; O'Hare *et al*., 2007). In parallel with impacts on abundance and composition, herbivory and other factors may alter chalk river community structure more subtly. Studies in other systems have demonstrated that herbivory may directly and indirectly alter flowering in grazed plants which then impacts sexual reproduction (Barber *et al*., 2011; Brys *et al*., 2011). There is some limited field evidence that swans may reduce flowering in aquatic plants (O'Hare *et al*., 2007), but it is not known how widespread this process is or how it might be affected by other drivers of plant health and fecundity such as temperature and light availability (Sculthorpe, 1967).

In temperate zones, river plants exhibit seasonal cycles of growth and recession; growth is strong in spring (April-June), peak abundances are reached in July and declines occur thereafter (Owens & Edwards, 1961; Dawson, 1976). Swans use this resource seasonally, switching from riparian pasture in winter and spring to the river during summer and autumn (**Chapter 5**). Thus the relative importance of community drivers including herbivory should vary between phases of the plant growth cycle. In particular, it is expected that biotic factors will be more important in the later phases of the plant growth cycle, since at this time the densities of swans present on the rivers are higher and greater leaf abundance on riparian trees reduces light availability for aquatic plants (Dawson & Kern-Hansen, 1978; **Chapter 5**). Additionally, whilst herbivores reduce plant abundances within a year (Cyr & Pace, 1993; Milchunas & Lauenroth, 1993; **Chapter 2**), it is unclear whether such reductions carry-over into subsequent years. Herbivory can cause reallocation of resources from roots to above-ground tissues, reducing growth and survival of the plant in subsequent seasons (McNaughton, 1983; Nolet, 2004). River plants weakened in this way may find it difficult to survive the winter when growth conditions are poor and plants are vulnerable to winter floods (Dawson, 1976a; Armitage & Cannan, 2000; Bowes *et al*., 2005). Therefore, herbivory earlier in the year may affect overwintering plant survival and thus abundance in subsequent years.

In this study I test two hypotheses addressing how the single, additive or interactive effects of biotic and abiotic factors regulate plant community structure and function, measured as abundance, flowering and dominance of water crowfoot, and species richness and evenness. I considered two biotic factors, herbivory and riparian shading (*i.e.* competition for light with terrestrial plants), and two abiotic factors, water temperature and distance downstream of the river source, over three phases in the growth cycle of a chalk river plant community, growth-phase (May), peak-phase (July), and recession-phase (September). The first hypothesis (H_1) was that the relative importance of biotic factors in the regulation of plant community properties would increase in the later phases of the plant growth cycle. The second hypothesis (H_2) was that reductions in plant abundance associated with herbivory would carry-over into the following year and result in lower plant abundances.

4.3 Methods

4.3.1 Study sites

The River Frome (Dorset, UK) is a shallow (typically < 1 m depth) mesotrophic chalk river, within a catchment of 414 km^2 (Bowes *et al.*, 2005). The aquatic plant community is dominated by water crowfoot, with perfoliate pondweed (*Potamogeton perfoliatus* L.), Canadian pondweed (*Elodea canadensis* Michx.), horned-pondweed (*Zannichellia palustris* L.), blunt-fruited starwort (*Callitriche obtusangula* Le Gall), European bur-reed (*Sparganium emersum* Rehmann), river water-dropwort (*Oenanthe fluviatilis* Coleman), watercress (*Nasturtium officinale* Aiton), and Eurasian water milfoil (*Myriophyllum spicatum* L.) also present in greater abundances at sites further from the river source (Dawson, 1976a; O'Hare *et al*., 2007; **Chapter 3**). Twenty sites, each consisting of a 500 m length of river, were selected along a 44 km length of river between Maiden Newton (50°46'N, 02°34'W) and West Holme (50°41'N, 02°10'W). Sites were selected to be representative of the catchment in terms of land use, channel morphology, riparian tree species (*Salix spp*. and *Alnus glutinosa* L.), hydrology and sediment; all sites were on the main channel with ≥ 75 % gravel substrate, and bordered by terrestrial pasture fields.

4.3.2 Estimating required sample size

To derive an estimate of the sample size required to accurately measure plant biomass I undertook intensive biomass sampling at six sites in early March 2010. At each site 30 samples were taken; sampling protocol is detailed in the next section. Bootstrap resampling with replacement was used to derive the relationships between sample size and accuracy of measuring mean plant biomass. For each analysis, *n* samples were selected randomly from the datasets of dry mass (DM) abundance samples (g DM m^{-2}) and the mean was calculated. 10,000 iterations of this process generated a frequency distribution of mean biomass values derived from a sample size of *n*, from which the mean and 95 % confidence intervals were calculated, where R_{CI} was the range between the lower 5 and upper 95 percentiles of the Bootstrap frequency distribution. I calculated the percentage error of my biomass measurements by calculating R_{CI} as a percentage of the mean biomass for a given value of *n*; data from all sites were pooled to yield mean (± 95 % CI) values. Error decreased as sample size increased, but did not decrease below ± 37.6 % even where *n* = 30 (**Figure 4.1**). As the greatest decrease in error occurred as *n* increased from 1 to 10, I selected *n* = 10 for my main study as a compromise between accuracy and sampling effort.

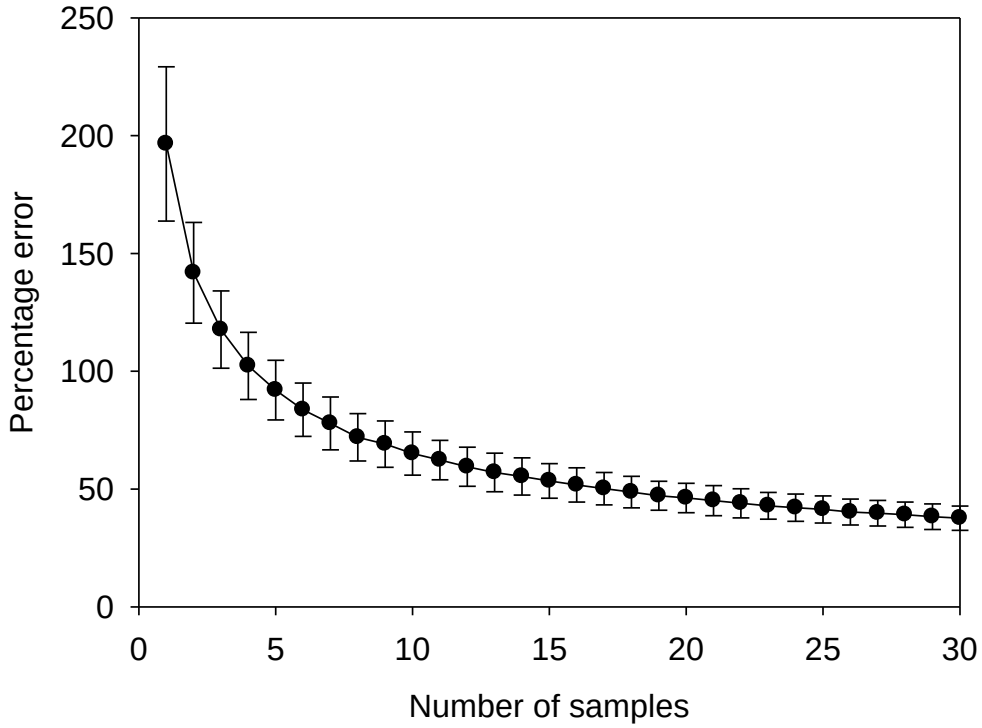


Figure 4.1: *The percentage error associated with estimates of mean biomass (g DM m^{-2}) for a given number of samples, based on the mean ± 95 % CI percentage error at six sites (n = 30 for each site).*

4.3.3 Plant abundance

Each month between March and September 2010, the mean percentage plant cover (± 5 %; all species) at each site was estimated visually from the river bank for 10 m reaches spaced equally over the site (two reaches per 100 m length of riverbank; total 10 reaches per site). Visual observations yielded estimates of plant cover that are strongly related ($R^2_{(adj)}$ = 59 %) to values gained by instream measurements, although there is a tendency for visual observations to overestimate cover by 27 % (**Chapter 3**). However, given that this overestimate is consistent across sites and months, it should not have influenced my ability to detect between-site and between-phase differences. At each site, 10 plant samples per month were taken using a 0.00785 m^2 cylindrical hand corer (**Chapter 3**). To select a 10 m reach for in-stream sampling, each 500 m site was divided into 50 equally sized sections, and each month a random number generator was used to select the biomass sampling reach. Within each, corer sampling locations were selected by generating random co-ordinates that were located in-stream (± 0.25 m) using fixed tape measures along the bank and across the river. For each core the centre of the plant stand closest to the co-ordinates was sampled. Biomass sampling locations were not fixed across months to minimise the risk of the removal of plant material influencing subsequent samples (Nolet, 2004). In the laboratory, non-plant material was discarded

and the sample dried to constant weight at 60 ˚C using a Heraeus Kelvitron T oven (Thermo Fisher Scientific, Loughborough, UK). Dry mass was measured (± 0.01 g) on a Sartorius PT120 balance (Sartorius GMBH, Germany).

4.3.4 Water crowfoot flowering

I recorded the percentage of water crowfoot stands on which flowers were observed at each site in each month between March and September 2010. I counted flowering stands at the reaches where plant cover was estimated and calculated the mean. As water crowfoot stands grow they frequently merge with other stands and move across the river bed in response to gradients in flow and sediment characteristics; thus distinct stands are not maintained across the season (Dawson, 1980; **Chapter 3**). Therefore, after the first incidences of flowering I were unable in any given month to distinguish between 'new' stands flowering for the first time and 'old' stands still flowering from the previous month. I adopted a conservative approach to stand independence in assuming that stands flowering in one month were also flowering in any subsequent months where flowering was observed at that location. Therefore I took the highest monthly percentage of stands flowering (F_{max}) as my estimate of flower abundance for that site; this approach was consistent across sites and thus should not have affected my ability to detect between-site differences.

4.3.5 Plant community composition

Estimates of community composition were based on plant percentage cover values. The percentage of the plant community comprised by water crowfoot is hereafter termed 'water crowfoot dominance'. Species evenness (J') per month at each site was calculated as:

$$J' = H / (\ln S)$$

where H is Shannon's diversity index and ln S is the natural logarithm of species richness (Pielou, 1966).

4.3.6 Biotic and abiotic variables

Surveys of each site were carried out monthly between February and September 2010. Swans present at each site were identified using a Swarovski STS 80HD (20 x 60) tripod-mounted telescope (Swarovski AG, Austria). Swans were aged as 'adult', 'juvenile', or 'cygnet' from plumage (Delany, 2005). Since variation in herbivore body mass may

confound analyses of herbivore impacts, herbivore grazing pressure was estimated as a biomass rather than numerical density (**Chapter 2**). Swan biomass density was estimated as the total (kg ha^{-1}) at each site in each month in that phase according to the formula:

$$\text{Swan biomass density} = ((\text{Count}_A \cdot \text{Mass}_A) + (\text{Count}_J \cdot \text{Mass}_J) + (\text{Count}_C \cdot \text{Mass}_C)) / A,$$

where Count_A, Count_J, and Count_C = total number of adults, juveniles, and cygnets respectively observed at the site during the month. Mass_A, Mass_J, and Mass_C = mean mass (kg) of adults (10.8 kg), juveniles (8.8 kg), and cygnets (May = 0. 3 kg, June = 2.8 kg, July = 5.5 kg, August = 7.3 kg, September = 8.8 kg) respectively (Bacon & Coleman 1986; Delany 2005). A = area (ha) of the site. Additional swan counts were carried out in January, March, May, July, September, and December 2009 as part of the test for carry-over effects of herbivory.

Water temperature and riparian shading were measured at each site in each month between March and September 2010 at the mid-point of the site (*i.e.* 250 m downstream of the upstream boundary). A thermometer (Breaksafe Thermometer, Brannan, UK) attached to a stake was placed in the middle of the river so that the tip of the thermometer was 0.15 (± 0.005) m beneath the water surface and not in contact with the stake. The thermometer was left in place for 20 (± 1) minutes after which the temperature value (± 0.5 °C) was recorded. As chalk rivers are predominantly groundwater fed they exhibit relatively small diurnal temperature fluctuations (Berrie, 1992). However, to minimise the confounding effects of any such fluctuations on the analyses, I avoided measuring temperature between 11:00 and 15:00, the warmest period of the day when air temperature is most likely to increase water temperature. Shading was estimated as the percentage (± 5 %) of the riverbanks covered by terrestrial vegetation ≥ 3 m in height at each site at which in-stream plant cover was estimated; I made 10 estimates of shading at each site, from which a mean value was calculated. Distance downstream (km) of the source (50°50'N, 02°36'W) was measured from Explorer Maps 117 and OL15 (Ordinance Survey, UK).

4.3.7 Statistical analyses

All statistical analyses were carried out using SPSS version 19 (IBM, US), with a statistically significant result attributed where $p < 0.05$. Normality of the residuals and homogeneity of variance were confirmed for all data with Kolmogorov-Smirnov and Levene tests respectively. To address effects on plant community properties (H_1) differences in (i) plant biomass (g DM m^{-2}), (ii) plant cover (%), (iii) F_{max} (%), (iv) water crowfoot dominance (%), (v) species richness, and (vi) species evenness, were tested

with General Linear Models (GLMs), with mean swan biomass (kg ha^{-1}), shading (%), temperature (°C) and distance from source (km) as covariates. Separate GLMs were carried out on each phase of the plant growth cycle, such that I used the mean values for that factor for the month of plant sampling and the two preceding months (*i.e.* for the growth-phase values were means of March, April and May). I allowed a one-month overlap, *i.e.* a partial 'sliding window' whereby May contributed to both growth- and peak-phases, whilst July contributed to both peak- and recession-phases. This sliding window acknowledges the soft boundaries between phases, as in reality May can comprise both growth- and peak-phases, whilst July can comprise both peak- and recession-phases (Dawson, 1976a). I tested all additive and two-way interaction terms, sequentially removing the least significant term until I achieved a final model that consisted only of significant terms. I used Pearson correlations to test for correlations between the explanatory factors; significantly correlated factors were not permitted in the same model; I modelled all combinations of uncorrelated variables and from these selected the model with the highest R^2_{adj} value as the best model. Linear regression analyses were used to test the relationships between (i) plant biomass (g DM m^{-2}) and (ii) plant cover (%) in March 2010 and mean swan biomass (kg ha^{-1}) in the previous 12 months (H_2).

4.4 Results

4.4.1 Spatiotemporal variation in biotic and abiotic factors

Mean (± 95 % CI) swan biomass densities increased from 21.8 ± 10.7 kg ha^{-1} in March to 116.7 ± 64.7 kg ha^{-1} in June, declining sharply to 70.9 ± 44.9 kg ha^{-1} in July before increasing slightly to 89.0 ± 57.8 kg ha^{-1} in September (**Figure 4.2a**). There was little temporal intra-site variation in riparian shading, which ranged between 5-45 % (**Figure 4.2b**). Mean water temperature increased from 10.2 ± 0.3 °C in March to 18.0 ± 0.6 °C in July, declining thereafter to 13.9 ± 0.3 °C in September (**Figure 4.2c**). Distances downstream ranged between 86.8-130.4 km from river source.

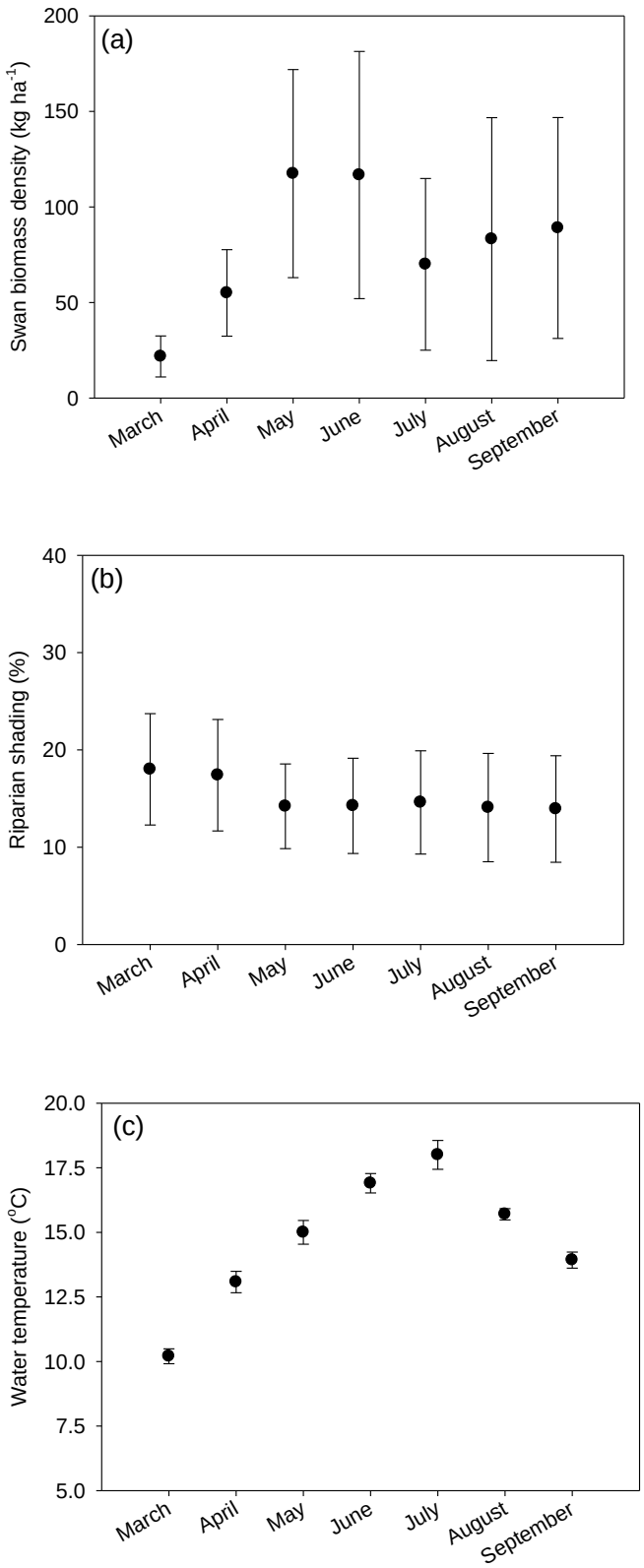


Figure 4.2: *Observed spatiotemporal variance in mean ± 95 % CI (a) swan biomass density, (b) riparian shading, (c) water temperature.*

For the growth-phase I detected that shading and temperature (r = 0.53, p = 0.015) and distance downstream and swan biomass density (r = 0.50, p = 0.027) were positively correlated. In contrast, shading and swan biomass density (r = -0.47, p = 0.036) and distance downstream and shading (r = -0.61, p = 0.005) were negatively correlated. For the peak-phase only a single negative correlation between distance downstream and shading was detected (r = -0.52, p = 0.019). This negative correlation between distance downstream and shading was also found for the recession-phase (r = -0.49, p = 0.028), as was a positive correlation between shading and temperature (r = 0.50, p = 0.024). For water crowfoot flowering negative correlations between shading and swan biomass (r = -0.47, p = 0.037) and distance downstream and shading (r = -0.52, p = 0.019) were found.

4.4.2 Effects of biotic and abiotic factors on the plant community

Mean (± 95 % CI) plant biomass increased from a March minimum of 38.5 ± 7.1 g DM m^{-2} to 576.4 ± 217.2 g DM m^{-2} in July, declining thereafter (**Figure 4.3a**). Plant biomass in the peak-phase decreased with greater shading in the peak-phase, and decreased with increasing swan biomass density and shading in the recession-phase (**Appendix 3**). Mean (± 95 % CI) plant cover increased from 16.1 ± 2.7 % in March to 52.7 ± 9.6 % in July, declining thereafter (**Figure 4.3b**). During the peak-phase, plant cover was negatively related to swan biomass density and positively related to distance downstream. Furthermore, there was an interaction between swan biomass density and temperature such that cover decreased with greater swan densities at low temperatures (≤ 14.3 °C) but showed no response to swan densities at higher temperatures. Finally, there was an interaction between temperature and distance downstream, such that cover decreased with temperature at low distances (< 110 km downstream of source), but had no effect at greater distances. As with plant biomass, cover was negatively related to swan biomass density and shading in the recession-phase (**Appendix 3**). However, no factors or interactions were statistically significant for the growth-phase.

Water crowfoot stands flowered between April and July, reaching a maximum of 26.7 ± 12.1 % in June (**Figure 4.3c**). There was a negative relationship between maximum monthly percentage of water crowfoot stands flowering (F_{max}) and swan biomass density (**Appendix 3**). Mean (± 95 % CI) water crowfoot dominance of the plant community decreased over the season, from 95.3 ± 4.5 % in March to 68.9 ± 9.2 % in September (**Figure 4.3d**). Whilst no models were significant for the growth-phase, dominance during both the peak- and recession phases declined with increasing temperature and distance; furthermore, there was an an interaction between temperature and distance such that dominance decreased with elevated temperatures at upstream sites (< 110 km from source) but increased with elevated temperatures at sites further downstream (**Appendix 3**).

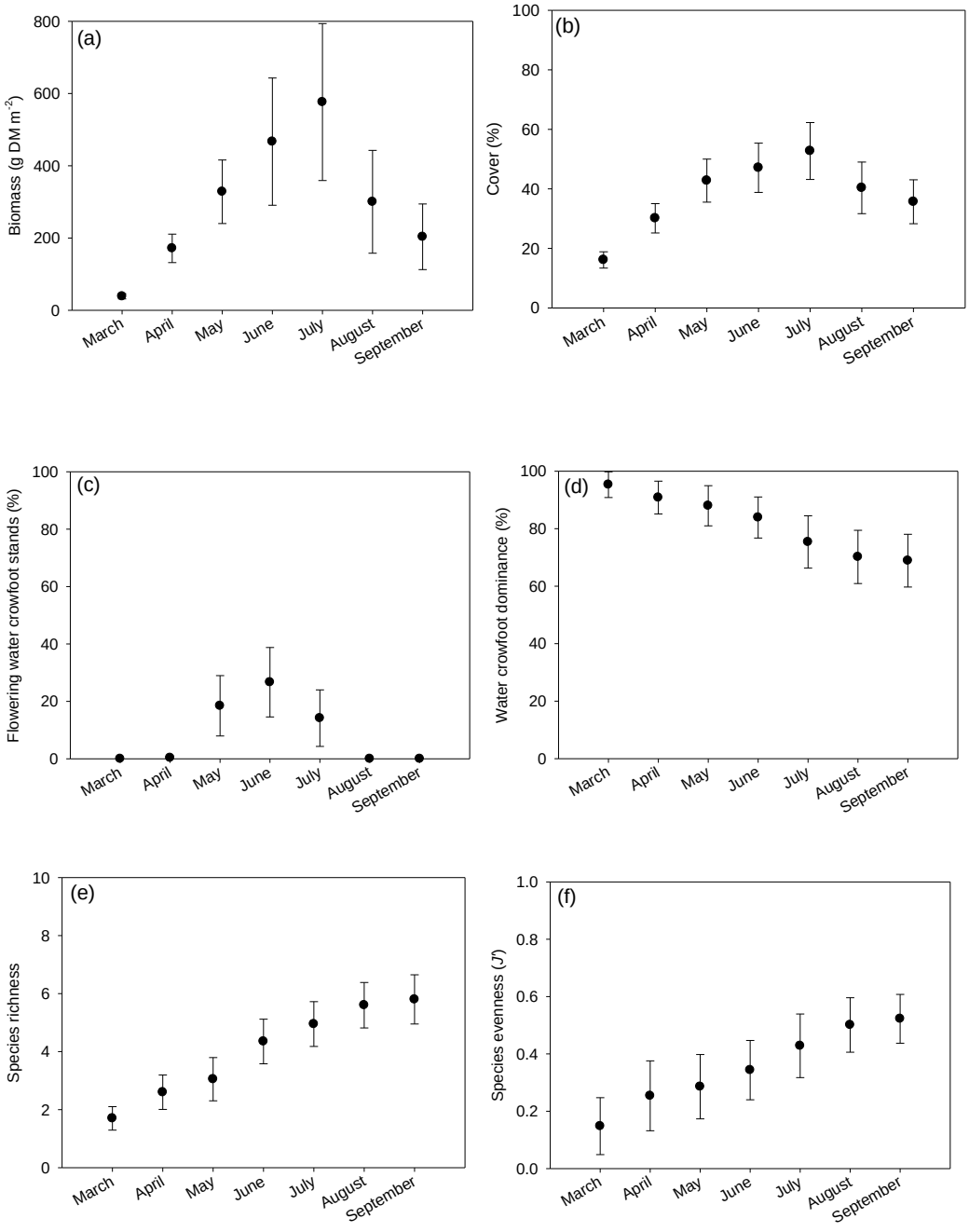


Figure 4.3: *Mean ± 95 % CI plant (a) biomass, (b) cover, (c) water crowfoot flowering, (d) water crowfoot dominance, (e) species richness, and (f) species evenness.*

Mean (± 95 % CI) species richness per site increased from 1.7 ± 0.4 in March to 5.8 ± 0.8 in September (**Figure 4.3e**). In the peak-phase richness increased with greater temperatures and distance downstream; I also detected an interaction between temperature and distance downstream, such that species richness increased with temperature at low distances (< 110 km downstream of source), but decreased with temperature at greater distances downstream. Species richness was positively related to distance downstream in the recession phase (**Appendix 3**). However, no models were statistically significant for the growth-phase. Mean (± 95 % CI) species evenness increased from 0.15 ± 0.10 in March to 0.52 ± 0.10 in September (**Figure 4.3f**). As with all other plant community metrics, no models were statistically significant for the growth phase. However, evenness was positively related to swan biomass density during the peak-phase. In the recession-phase, evenness increased positively with temperature and with distance downstream, with an interaction between temperature and distance, such that evenness increased with temperature at low distances (< 110 km downstream of source), but decreased with temperature at greater distances downstream (**Appendix 3**).

4.4.3 Carry-over effects of herbivory

No relationship was found between mean plant biomass in March 2010 and mean swan biomass density at that site in the previous year (March 2009 to February 2010) ($F_{1,18}$ = 0.51, p = 0.48, $R^2_{(adj)}$ = 0.0 %; **Figure 4.4a**), or between mean plant cover in March 2010 and mean swan biomass density at that site in the previous year (March 2009 to February 2010) ($F_{1,18}$ = 0.41, p = 0.53, $R^2_{(adj)}$ = 0.0 %; **Figure 4.4b**).

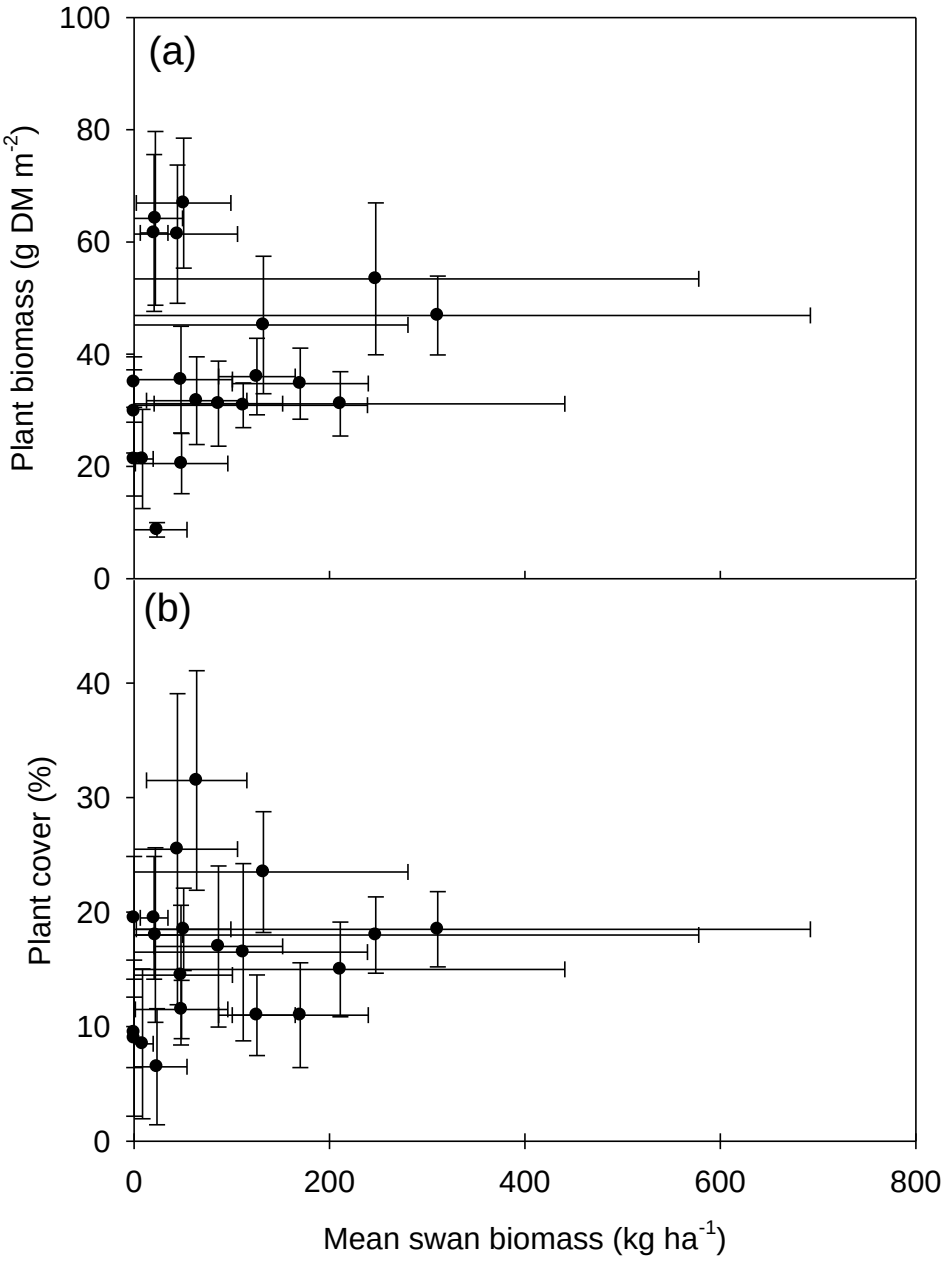


***Figure 4.4**: The mean ± 95 % CI plant (a) biomass and (b) cover in March were not related to the mean ± 95 % CI swan biomass (kg ha^{-1}) in the previous year.*

4.5 Discussion

My results demonstrate that whether factors singularly, additively or interactively regulate plant community structure and function depends strongly on the phase of the plant growth cycle. Previous research on relative biotic and abiotic regulation of plant communities has largely ignored within-year cycles of plant growth and recession, despite the ubiquity of such cycles in temperate ecosystems (Gu *et al*., 2009). The influence of distance from river source on the plant community highlights the importance of considering spatial, as well as temporal, patterns in plant community structure and function. Whilst the effects of herbivory were important within a year, I found no evidence that such effects carried over into subsequent years in contrast to many other plant-herbivore studies (McNaughton, 1983; Milchunas & Lauenroth, 1993). Quantifying the range of plant community responses to multiple biotic and abiotic factors is critical to understanding the impact of environmental change on plant-dominated ecosystems (Rietkerk *et al*., 2004; Bowes *et al*., 2012).

Swan herbivory reduced plant abundance in the peak- (cover) and recession- (biomass and cover), but not growth-, phases of the plant growth cycle, providing support for my first hypothesis (H_1). In chalk river catchments most swans spend the winter and spring in the terrestrial pasture fields adjacent to the river, entering the river in late April or early May (O'Hare *et al*., 2007; this study; **Chapter 5**). Thus herbivory became a more important regulatory factor when swan biomass densities increased during the peak- and recession-phases. This led to substantial reductions in plant abundance. Similar observations are reported for other aquatic ecosystems (Hidding *et al*., 2010; **Chapter 2**). Additionally, the growth rates of plants, and thus their ability to replace tissues lost to herbivory, are greater during the growth-phase compared with the peak- and recession-phases (Dawson, 1976a). The swan density-temperature interaction may indicate that at low temperatures losses of plant cover due to swans were partially offset by increased growth of water crowfoot, the dominant species. Water crowfoot productivity is negatively related to water temperatures, so at higher temperatures this compensatory effect would have been lost (Dawson *et al*., 1981).

The strong negative effect of riparian shading on plant biomass (peak- and recession-phases) and cover (recession-phase) demonstrates that light-limitation is a key determinant of lotic plant abundances in the later phases of the growth cycle. Reduced light availability, due to competition for light with riparian vegetation, inhibits photosynthetic activity and thus growth of higher plants and regulates algae communities too which, suggests that light availability is a key determinant of structure and function across aquatic ecosystems (Owens & Edwards, 1961; Dawson & Kern-Hansen, 1978;

Weisner *et al*., 1997; Jones & Sayer, 2003; Bornette & Puijalon, 2011; Bowes *et al*., 2012). Whilst intra-site variation in water temperature was small, which is typical of groundwater-fed chalk rivers (Berrie, 1992), sites with higher temperatures typically had higher plant cover in the peak-phase, probably due to increased photosynthetic activity and thus growth, particularly in pondweed species (Pilon & Santamaria, 2001; Bornette & Puijalon, 2011). However, increased temperatures could have a slightly negative effect on plant cover at the sites closest to the source, as indicated by the distance downstream-temperature interaction in the peak-phase. Increased temperatures are known to inhibit growth of water crowfoot, which is most dominant within the plant community at sites closer to the river source (Dawson *et al*., 1981). Thus sites further downstream, with greater proportions of species which benefit from higher temperatures, such as perfoliate pondweed, blunt-fruited starwort and Canadian pondweed, were less affected by increased temperature (Barko *et al*., 1982; Pilon & Santamaria, 2001). As a parameter in the analyses, distance downstream was a proxy for the complex changes in morphology, hydrology and nutrient status that occur between upstream and downstream sites in a river catchment (Hilton *et al*., 2006); as such, it is difficult to determine the precise mechanisms by which distance downstream positively affected plant cover during the peak phase. In shallow rivers downstream sites typically have greater discharge, depth, nutrient concentrations, and channel width and a lower bed surface slope and water velocity (Berrie, 1992; Cotton *et al*., 2006; **Chapter 3**). Higher nutrient concentrations found at downstream sites are likely to favour the growth of pondweed species over water crowfoot (Spink *et al*., 1993); the inclusion of larger-leaved pondweed species in the plant community may in part explain the higher observed plant cover at the downstream sites. At depths exceeding 0.35 m, water crowfoot biomass is known to be negatively related to depth due to reduced light availability (Dawson, 1976a); the depth at many of the downstream sites in this study certainly exceeded this threshold. Plant abundances in chalk rivers are known to decrease in response to low velocities, but the relationships with many of these other factors are less clear (Owens & Edwards, 1961). Further studies, which measure these factors directly and relate them to changes in plant community structure and function are required. The two measures of plant abundance were regulated by similar suites of factors, although the percentage of variance explained by the best model was consistently greater for cover compared with biomass.

Flowers are typically one of the most nutrient-rich plant tissues, which makes them an attractive food for herbivores (Barber *et al*., 2011; Brys *et al*., 2011); thus it was unsurprising that increased herbivory decreased the percentage of stands flowering. The distance downstream-temperature interaction was found to influence water crowfoot dominance (peak- and recession-phases), species richness (peak-phase) and species evenness (recession-phase), increasing community diversity at upstream sites by increasing the relative competitiveness of species such as pondweeds and starwort,

which would otherwise be excluded by water crowfoot (Dawson *et al*., 1981; Barko *et al*., 1982; Pilon & Santamaria, 2001). Lower dominance of water crowfoot and greater species richness during the peak- and recession-phases were promoted by factors that tended to suppress the growth of the dominant macrophyte species; greater temperature and distance downstream have both previously been shown to depress water crowfoot growth and thus increase the relative competitiveness of other plant species (Dawson *et al*., 1981; Pilon & Santamaria, 2001). Presumably these effects also underpin the observed increases in species evenness at sites during the recession-phase which had higher temperatures and were further downstream. However, earlier in the growth cycle during the peak-phase, species evenness was related positively to swan biomass density, suggesting grazing of the more naturally-abundant species. During the growth-phase few plant species were present, as typically only water crowfoot overwinters above-ground (Owens & Edwards, 1961; Dawson, 1976a). Thus changes to plant abundances during the growth-phase did not translate into community-level effects. During the peak-phase a greater number of species became established, thus reductions in the abundances of dominant palatable species at grazed site produced a more even community. However, by the recession-phase all species were declining in abundance and thus grazing losses did not alter evenness.

In only four instances did the best models explain > 50 % of between-site variance, indicating that other factors likely affected plant community structure. In shallow rivers channel substrate is known to affect plant communities and may have contributed to the unexplained variance (O'Hare *et al.*, 2011). Measurements of aquatic plant abundance are often associated with considerable error (**Chapter 3**; this chapter); whilst I quantified the error associated with the abundance measurements, such error likely introduced at least some additional variance into the data.

A standard approach used to quantify herbivore effects on plant abundance in lakes and terrestrial ecosystems is the use of herbivore exclosures, with comparisons of the plant community within (herbivores absent) and outside (herbivores present) the exclosures (Wass & Mitchell, 1998). However, I elected to use a comparison of naturally ungrazed and grazed river reaches (after O'Hare *et al*., 2007), along a gradient of herbivore biomass densities, for two key reasons: (i) exclosures in flowing waters would collect coarse organic material, which could reduce light availability and modify patterns of water flow within the exclosure, thereby affecting the plant community and confounding estimates of swan effects (Dawson, 1976b); (ii) as swans can reach with their neck to an extent of around 70 cm (Owen & Cadbury, 1975), to prevent the swans reaching into the exclosures I would have had to either used a large exclosure, which would have been

inconvenient to other river users such as anglers, or use an exclosure with gaps in the exclosure which were small enough to prevent a swan passing its head through, which would have increased flow impedance and debris collection. The potential problem with my methodology was that there may have been confounding differences in the factors which affect the plant community between the ungrazed and grazed areas. Therefore I attempted to minimise this risk by quantifying these confounding factors, temperature, shading and distance downstream, and analysing how and when they affected the plant community.

The lack of carry-over of reductions in plant abundance from the previous year may be linked to the elevated river discharge observed during the winter. Winter discharge, which is typically five times greater than the summer and autumn (Armitage & Cannan, 2000; Bowes *et al*., 2005), removes large quantities of plants and prevents regrowth above a maximum biomass of approximately 50 g m^{-2} (Dawson, 1976a; **Chapter 3**). As swan grazing does not remove plant roots (O'Hare *et al.*, 2007), grazed sites can recover during this winter period of elevated discharge when most swans have left the river. In contrast, ungrazed sites, whilst typically having greater plant biomass, will have biomass reduced due to 'wash-out' associated with elevated discharge (Armitage & Cannan, 2000). Therefore, contrary to the predictions of my second hypothesis (H_2), the regulation of plant abundance by river discharge during winter offsets any reductions in plant abundance due to swan grazing in the previous season.

This study demonstrates that biotic and abiotic factors can singly, additively and interactively regulate shallow river plant community structure and function. In particular, the contrasting effects of temperature on plant cover illustrate the importance of analysing how the effects of a given variable on the plant community may vary depending on the phase of the plant growth cycle, the magnitude of other variables, and the identity of the species which comprise the community. For example, Bullock *et al*. (2001) found that the effects of grazing by sheep (*Ovis aries* L.) on mesotrophic grassland species richness could be positive, neutral or negative depending on the time of year and herbivore densities. In this study a single plant community was found to be regulated by combinations of top-down (*e.g.* herbivory), bottom-up (*e.g.* temperature, downstream effects), and competitive (*e.g.* riparian shading) factors. Different suites of factors regulate different properties of the plant community in different phases of the the plant growth cycle; as such, these results highlight the need to consider seasonal patterns of growth and recession when investigating determinants of plant community structure and function.

Chapter 5: Seasonal variation in the structure, reproduction and habitat use of a mute swan (*Cygnus olor*) population in a chalk river catchment.

5.1 Abstract

Conflicts have been reported between mute swans and agricultural, fisheries, and conservation interests in chalk river catchments in Britain, due to grazing of vegetation by flocks of swans. However, attempts to alleviate such conflicts have been hindered by a lack of data on the structure, reproduction, and habitat use of chalk river swan populations. I use data from repeat surveys of the River Frome (Dorset, UK) over two years to address this deficit. Seasonal variation in social structures was identified, with larger absolute and relative numbers of individuals living in non-territorial flocks in the winter. The sex ratio was close to parity. Reproductive output was low, with immigration from other catchments providing a winter influx of individuals. I demonstrated a strong seasonal switch in habitat use, with pasture preferred in spring and winter, and river preferred in summer and autumn. My results suggest that it will not be possible to manage the flock subpopulation, for which grazing conflicts have been reported, without also affecting the breeding subpopulation, for which no such conflicts have been reported. Removal of swans within the catchment, for example through translocation, may be offset by immigration. Thus, habitat management, rather than population management, may be a more effective means of alleviating conflicts with mute swans.

5.2 Introduction

Mute swans (*Cygnus olor* Gmelin, 1789) are large, herbivorous birds capable of consuming up to 4 kg of fresh vegetation daily (Mathiasson, 1973). Native to Europe and Asia, Mute Swans have been spread by humans beyond this range to establish populations in North America, Australasia, and South Africa (Birkhead & Perrins, 1986). Over much of their geographic range mute swans are popular with the public and are thus regarded as a charismatic species (Birkhead & Perrins, 1986). However, mute swans can be a source of conflict with human activities and conservation aims; swans can damage both crops and natural plant communities through consumption, trampling and faecal contamination (Parrott & McKay, 2001a; O'Hare *et al.*, 2007), and may displace other waterbirds through competition and aggression (Conover & Kania, 1994).

In Britain, chalk river catchments support diverse and productive wildlife communities as well as economically valuable agriculture and game fishing (Environment Agency, 2004). In these catchments conflicts with mute swans have been reported for both terrestrial and aquatic habitats (Trump *et al.*, 1994). The mute swan population in Britain has recently undergone a substantial increase from 17,600 individuals in 1978 to 31,700 in 2002 (Ward *et al.*, 2007). Over the same period concerns have been raised by riparian stakeholders regarding damage to both pasture grasses and aquatic plants (Harrison, 1985; Trump *et al*., 1994; O'Hare *et al*., 2007). Harrison (1985) demonstrated a mean pasture grass yield loss of 11.4 % in fields grazed by flocks of swans, increasing livestock feed costs for the farmers affected. O'Hare *et al*. (2007) reported a 49.2 % reduction in aquatic plant biomass due to grazing by a flock. Losses of aquatic plants due to grazing are known to reduce the value of river reaches as sport fisheries (Fox, 1994). Given these negative ecological and socioeconomic effects of swan grazing, there is a need to alleviate the grazing conflict through management.

Management of swan grazing conflicts requires knowledge of the spatiotemporal variance in the foraging ecology, population structure (*i.e.* age and social structure and sex ratio), reproduction, and habitat use of swans (Chisholm & Spray, 2002; Spray *et al*., 2002). In particular, ecological models which predict the outcomes of different conflict management strategies rely on the availability of such foraging and demographic data (*e.g.* Watola *et al*., 2003; Ellis & Elphick, 2007; **Chapter 6**; **Chapter 8**). Previous studies have made progress in understanding swan foraging ecology and the interactions between swans and their food plants (Mathiasson, 1973; O'Hare *et al*., 2007). However, recent attempts to assess the efficacy of population management (Watola *et al*., 2003) and habitat modifications (Parrott & McKay, 2001b) in chalk rivers have been limited by a lack of data on swan structure, reproduction and habitat use.

An understanding of the spatiotemporal variation in size and structure of the grazer population is necessary because reductions in plant biomass increase with waterfowl biomass densities (**Chapter 2**); therefore, the grazing conflict in a given area may be greater for flocks that are larger and older (as adult swans are typically heavier than juveniles; Birkhead & Perrins, 1986; Delany, 2005). Thus, in order to accurately predict waterfowl-plant interactions a model requires data on the relative abundance of different age groups. Ecological models used to predict the population-level consequences of different management techniques typically assume an equal sex ratio (Watola *et al*., 2003; Ellis & Elphick, 2007), but this assumption has yet to be tested for chalk river mute swans. Thus, data on the social and age structures and sex ratios of chalk river mute swan populations are required.

Efforts to alleviate grazing conflicts with waterfowl frequently employ clutch manipulation techniques, such as egg oiling or pricking, to reduce productivity and thus reduce grazer populations (Wright & Phillips, 1991; Baker *et al*., 1993). To predict the efficacy of such techniques, the breeding population size (*i.e.* the number of pairs within an area which breed, or attempt to breed) and the productivity (*i.e.* the number of eggs laid and how many cygnets are hatched and fledged) should be measured. An understanding of territory size and breeding densities would also help determine the effort managers should devote to searching for nests. Whilst data have been obtained for the River Avon and its main tributary the River Wylye (Hampshire and Wiltshire, UK), this chalk river catchment is suspected to be subject to illegal efforts to control swan numbers, including the removal and destruction of eggs (Trump *et al*., 1994; Watola *et al*., 2003). Thus, no data on the breeding population size or productivity exist for an un-manipulated chalk river swan population.

In chalk river catchments reports of swan conflicts have suggested that terrestrial conflicts occur in winter, whilst aquatic conflicts typically occur in summer (Trump *et al.*, 1994; O'Hare *et al.*, 2007; **Chapter 4**). The reasons for such distinct seasonal patterns of conflict in chalk river catchments are unclear. They may results from seasonal switches in habitat use as documented for other ecosystems (Chisholm & Spray, 2002; Nolet *et al*., 2002). Alternatively, the timing of conflicts in each habitat could result from periods of plant sensitivity to herbivory, in particular periods of plant colonisation or low abundance (Marklund *et al*., 2002).

In this study I used data from repeated surveys over two years to address three objectives regarding the structure, reproduction and habitat use of a mute swan population in a chalk river catchment. My first objective was to quantify swan population structure across different seasons by quantifying the age and social statuses as well as the sex ratios. My second objective was to assess the breeding population size and productivity of an unmanaged mute swan population. My third objective was to quantify swan habitat use and identify any seasonal switches.

5.3 Methods

5.3.1 Study area

This study was undertaken in the catchment of the River Frome (Dorset, UK), a mesotrophic chalk river that flows through a landscape used primarily for mixed pastoral and arable agriculture. The main river channel, and associated side streams, are dominated by the aquatic plant water crowfoot *Ranunculus penicillatus ssp. pseudofluitans* (Syne) S.D. Webster (O'Hare *et al.*, 2007). The river is typically bordered by pasture fields dominated by perennial ryegrass (*Lolium perenne* L.), creeping bentgrass (*Agrostis stolonifera* L.), and Yorkshire fog (*Holcus lanatus* L.), and small patches of damp woodland of black alder (*Alnus glutinosa* L.) and willow (*Salix spp.*). Drainage ditches, often connected to the main river channel, frequently separate pasture fields. Numerous shallow lakes are also found within the catchment.

5.3.2 Catchment surveys

Surveys of the River Frome catchment, including the main tributary the River Piddle, were carried out in January, March, May, July, September, and December 2009, and monthly between February and November 2010. On each occasion the river and the adjacent land approximately 500 m either side, including any other waterbodies, were surveyed from the Wareham Channel estuary (50°43'N, 02°02'W) 56.5 km upstream to Maiden Newton (50°46'N, 02°34'W) on the River Frome, and 12.0 km to Warren Heath (50°43'N, 02°12'W) on the River Piddle. Swans were identified using a Swarovski STS 80HD (20 x 60) tripod-mounted telescope (Swarovski AG, Austria); for each individual the location, age category (adult, juvenile, or cygnet), social grouping (flock, breeding, lone), and habitat (pasture, river, lake, ditch, estuary, arable, woodland or urban) were recorded. Cygnets (≤ 6 months old) had greyish-brown plumage; juveniles (7-18 months old) possessed pinkish-grey bill colouration and some greyish-brown feathers; adults (> 18 months old) possessed all-white plumage and orange bill colouration (Birkhead & Perrins, 1986; Delany, 2005). Beyond simple differentiation of adults, juveniles, and cygnets, precise age determination of swans is not possible (Birkhead & Perrins, 1986). To reduce subjectivity all surveys were undertaken by a single observer. Swans were considered to be flock birds if they were observed to be within 20 m of another swan, with at least three individuals present. To quantify breeding population size, in 2010 I recorded nest location and territory size for each pair that exhibited territorial behaviour (*sensu* Birkhead & Perrins, 1986). I also recorded the sizes of clutches (number of eggs laid) and broods (number of cygnets hatched), and the number of cygnets fledged, *i.e.* survived until September (Birkhead & Perrins, 1986; Kear, 1988). Due to their large size and white plumage mute swans are highly conspicuous and thus detection probability for breeding pairs has been shown to be around 0.94 (Gayet *et al*., 2011a). Territory size was

estimated as the maximum area over which the pair or family group was observed to range over the breeding season (March to September), based on repeated monthly site visits (after Scott, 1984). To estimate the sex ratio of the population I used resightings of marked individuals of known gender. Some individuals had been fitted with coloured leg rings engraved with a unique three-character alphanumerical code (Ogilvie, 1972) as part of a long-term swan mark-recapture programme in the south of England, ongoing since the 1970s (see Watola *et al.*, 2003). Where ringed individuals were observed during surveys the code was recorded and the sex of these individuals, determined at ringing by cloacal analysis (Birkhead & Perrins, 1986), were provided by the local swan ringing groups. Swans were ringed during their annual moult, which occurs for both sexes in the same period (July to August), thus there were no differences in the capture probability of males and females which could have biased my estimate of the sex ratio (Birkhead & Perrins, 1986). Each catchment survey took four days, and was only conducted during daylight hours. Whilst I cannot exclude the possibility that swan movements during a survey may have resulted in individuals being either undetected or double-counted, the fact that no ringed individual was ever observed twice during the same survey suggests that this was unlikely.

To quantify habitat availability, the area of each habitat category was recorded (± 0.001 km^2). Habitat preferences were examined by electivity analysis. For each month for each habitat category, Ivlev's electivity index (*s*) was calculated as:

$s = (a - b) / (a + b)$

where *a* is the percentage of the population using a given habitat, and *b* is that habitat as a percentage of the total habitat available (Jacobs, 1974). Electivity values represent the relative habitat use of a species; values range between -1.0 (habitat never used) and +1.0 (habitat exclusively used), with 0.0 representing habitat used in proportion with its availability (Jacobs, 1974).

5.3.3 Statistical analyses

Analyses were carried out using SPSS version 19 (IBM, US), with a statistically significant result attributed where $p < 0.05$. Normality of the residuals were confirmed with Kolmogorov-Smirnov tests. For comparisons of between-season effects, I sorted monthly mean values into groups on the basis of season; spring (March, April), summer (May, June, July, August), autumn (September, October), or winter (November, December, January, February). All such monthly mean values, grouped according to season, were used in a linear mixed effects model to test the effects of season and swan group (flocks or breeders) on electivity for (i) pasture, (ii) river, (iii) lake, (iv) ditch, (v) estuarine, and (vi)

arable habitat. Electivity values were rescaled between 0 and 1, and arcsine square root transformed to meet the assumptions of the mixed effects model. Season and social group were set as fixed effects, with year specified as a random effect. The breeding subpopulation was defined as the sum of paired and family adults within a survey.

5.4 Results

5.4.1 Structure

The Frome catchment had a mean (± 95 % CI) population of 298.2 ± 18.9 swans, with the population size typically highest in winter and lowest in spring and autumn (**Figure 5.1**). A total of 215 ringed birds were observed; based on the 88 ringed swans whose sex was known the proportion (and binomial 95 % confidence interval) of males was 0.49 (0.39 – 0.59) and of females was 0.51 (0.41 – 0.61). The majority of mute swans were observed in flocks (61.0 ± 4.1 %), with smaller percentages of paired individuals (18.4 ± 3.9 %) and birds in family groups (16.8 ± 5.9 %), and few swans observed alone (3.9 ± 0.9 %). The number of flock birds was greatest in winter (range: 176 to 264) and lower in spring (196 to 210), summer (146 to 193) and autumn (110 to 147). Correspondingly, a greater mean (± 95 % CI) number of flocks was observed during winter (18.8 ± 4.4) relative to spring (11.7 ± 5.3), summer (8.2 ± 2.0) or autumn (10.7 ± 2.4), but mean (± 95 % CI) flock size was relatively stable at 17.7 ± 4.5 individuals. Swans in breeding groups were most numerous in summer and autumn, but never decreased below 70 individuals outside of this period. The number of lone birds was highest in late winter (January-February) and lowest in summer. The total population was principally composed of adults (mean = 66.1 ± 3.8 %), with smaller mean proportions of juveniles (22.8 ± 4.4 %) and cygnets (11.1 ± 4.8 %) (**Figure 5.2a**). Similarly adults dominated flocks, comprising 62.9 ± 5.8 % compared with 34.9 ± 6.8 % juveniles and 2.1 ± 2.8 % cygnets (**Figure 5.2b**).

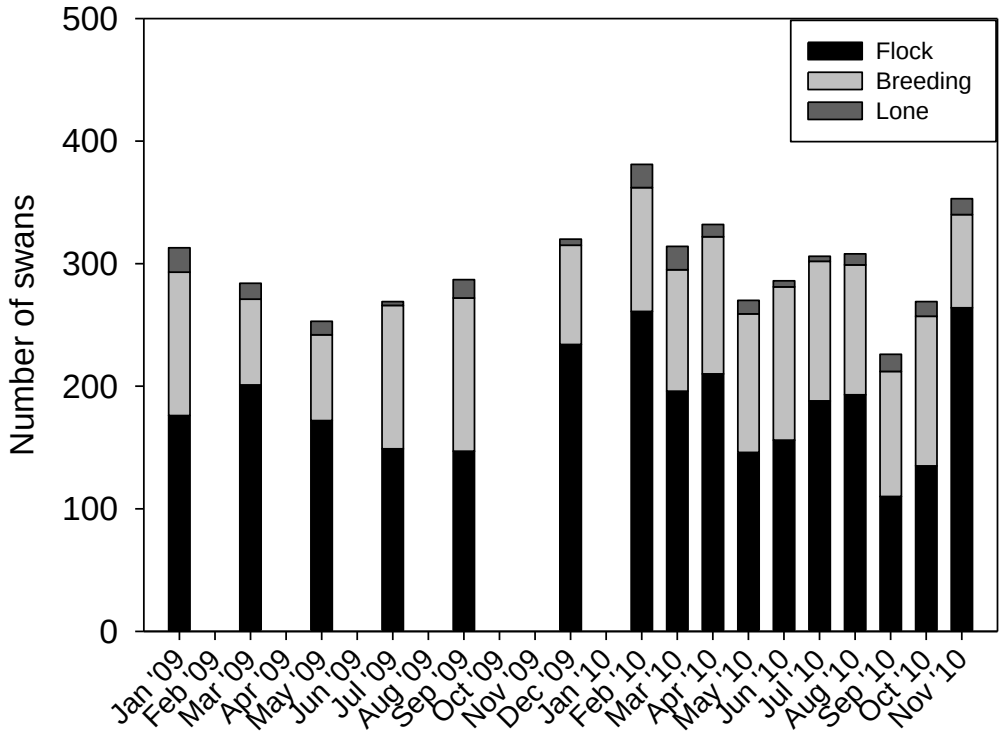


Figure 5.1: *Temporal variation in the social structure of the River Frome mute swan population.*

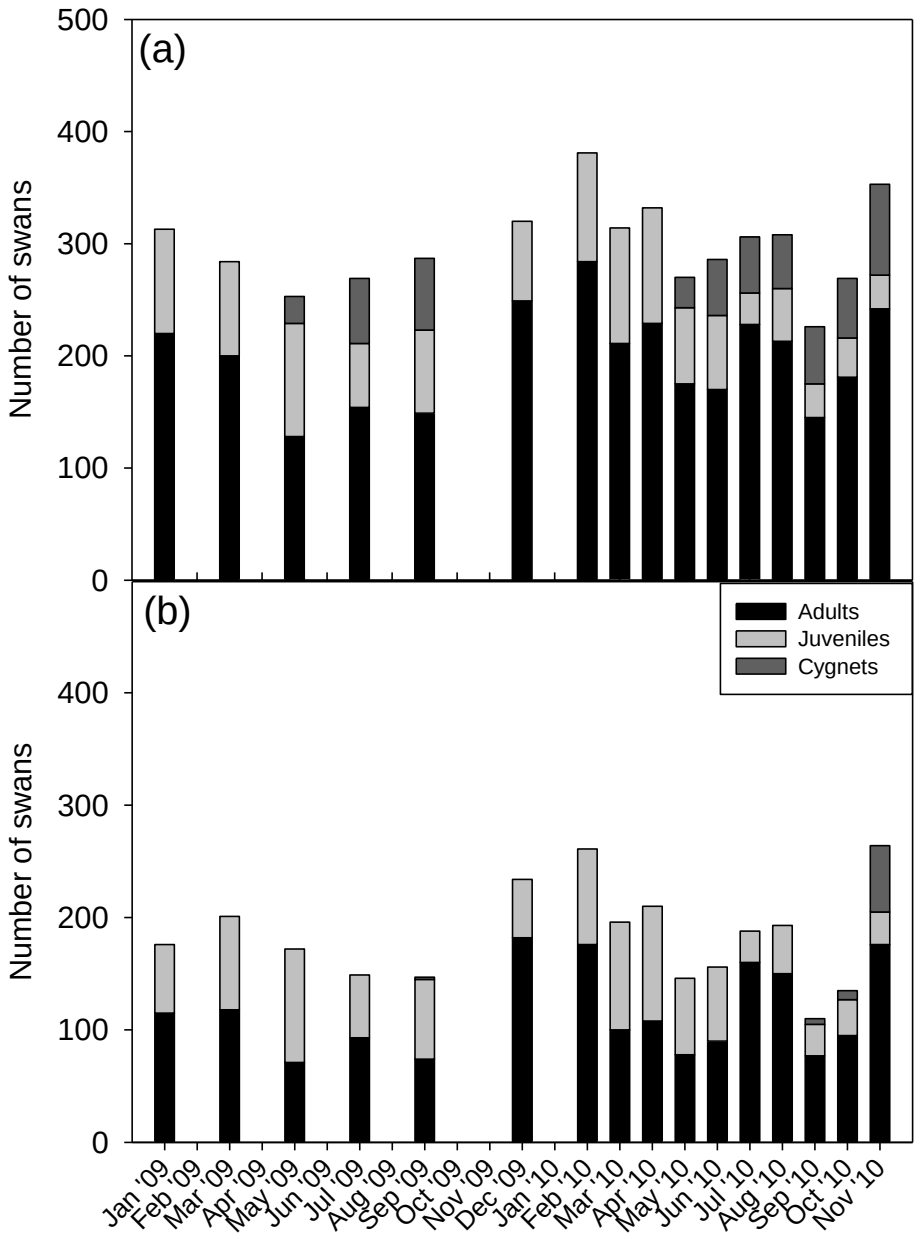


Figure 5.2: *Temporal variation in the age structures of the (a) total population and (b) flock subpopulation.*

5.4.2 Reproduction

Considering the number of swans that were of breeding age (*i.e.* ≥ 2 years; Birkhead & Perrins, 1986) the number of swans that actually attempted to breed was low (**Figure 5.3**). Despite the presence of 229 sexually mature adults in April 2010, only 112 formed a pair and 39 of these pairs established a territory. Nests were built by 36 pairs, with 25 pairs laying at least one egg, 21 pairs successfully hatching at least one egg and 20 pairs

successfully fledging at least one cygnet. Not all nests were detected and thus the data presented below do not contain reproductive parameters for all pairs; in each case the relevant sample size is given. Where nesting attempts were successful and eggs were laid, mean clutch size was 4.8 ± 1.2 (*n* = 18). Where all nests are considered, including those where no eggs were laid, mean number of eggs per nest was lower at 3.9 ± 1.2 (*n* = 22). Of the pairs whose reproductive success was known, mean survival of cygnets from egg to fledging (*i.e.* September) was 37.3 ± 16.7 % (*n* = 18). Mean territory size of nesting pairs was 0.0085 ± 0.0022 km^2 (*n* = 28), which corresponded to a 0.77 ± 0.18 km length of river. Thus the breeding density over the 68.5 km of river studied was 1 pair per 2.45 km. The total number of cygnets fledged within the catchment was 64 in 2009 and 74 in 2010.

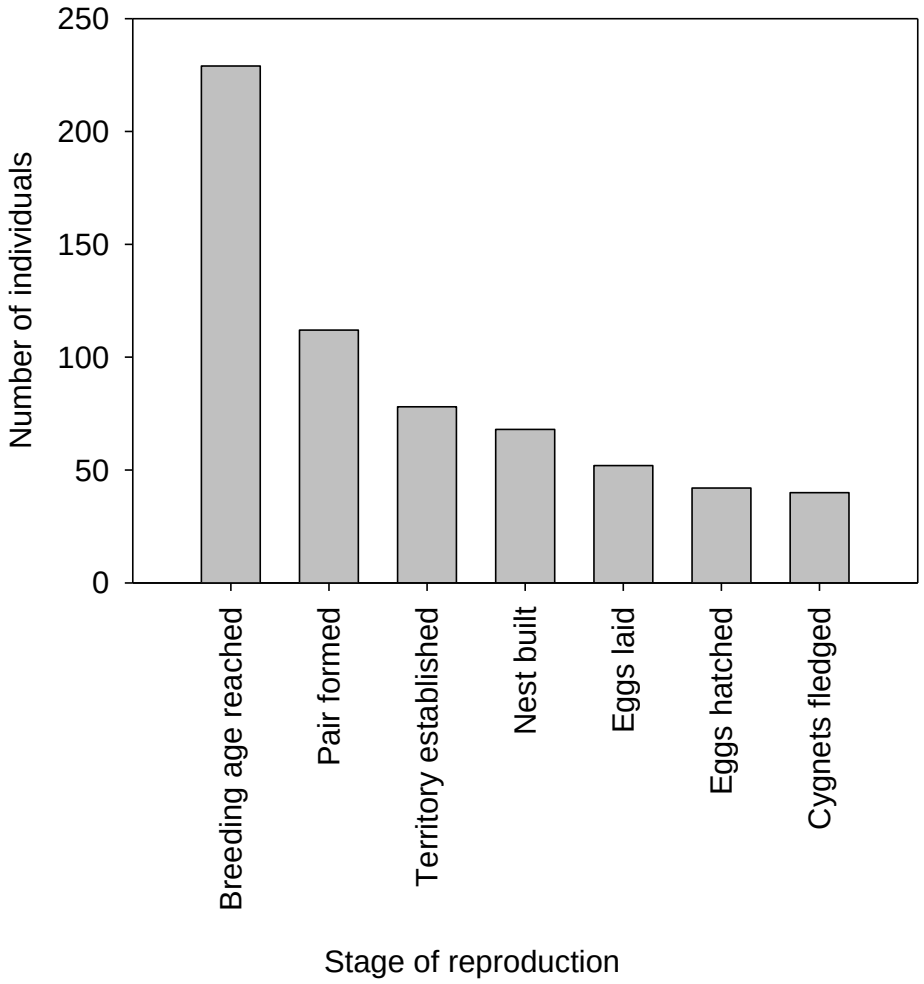


Figure 5.3: *The number of individuals achieving each of the major stages of reproduction.*

5.4.3 Habitat use

Comparisons of habitat availability and use by swans suggested that habitats were not used in proportion to their availability (**Table 5.1**); in particular, the river was preferred in summer and pasture preferred in winter and spring. Estuarine habitat was important in the summer as the principal moulting site in the catchment. Urban and woodland habitat constituted 15.1 % and 7.7 % of the available habitat respectively, but no swans were ever observed in either habitat. The percentage of river length used by flocks was 19.9 % in 2009 and 22.1 % in 2010, whilst the percentage of pasture fields used by flocks was 10.2 % in 2009 and 9.4 % in 2010. Habitat electivity values differed significantly both between seasons and between social grouping for pasture, river and estuarine habitat (**Table 5.2**). Electivity for river habitat as greater in summer and autumn relative to winter and spring, whilst the reverse pattern was observed for pasture (**Figure 5.4**). Non-breeding individuals switched from pasture to river between April and May, and from river to pasture around October (**Figure 5.5**). Electivity was greatest for estuarine habitat in summer. Additionally, electivity differed significantly between social groups for lake and ditch habitats. Breeders had a stronger preference for river, ditch and lake habitats relative to flocks, whilst flocks had the stronger preference for pasture and estuarine habitat. However, electivity for arable habitat did not differ between seasons or social group. As a random effect year explained 0 % of the residual variance for river, lake and ditch, 2 % for estuary and 9 % for pasture habitats. However, year explained a greater percentage of the residual variance for arable habitat (21 %), although arable habitat was highly avoided by both social groups in all four seasons in both 2009 and 2010.

Table 5.1: *A comparison of the availability and use of six habitats by the mute swan population in the River Frome catchment.*

Habitat type	**Habitat availability (%)**	**Habitat use by total swan population (%)**			
		Spring	**Summer**	**Autumn**	**Winter**
Pasture	46.1	67.0	6.6	17.3	80.1
River	4.5	15.9	61.7	72.7	10.2
Lake	1.0	11.4	2.2	3.2	3.5
Ditch	3.4	1.8	1.6	1.0	3.0
Estuary	10.3	1.4	27.8	5.9	1.4
Arable	11.9	2.5	0.0	0.0	1.7

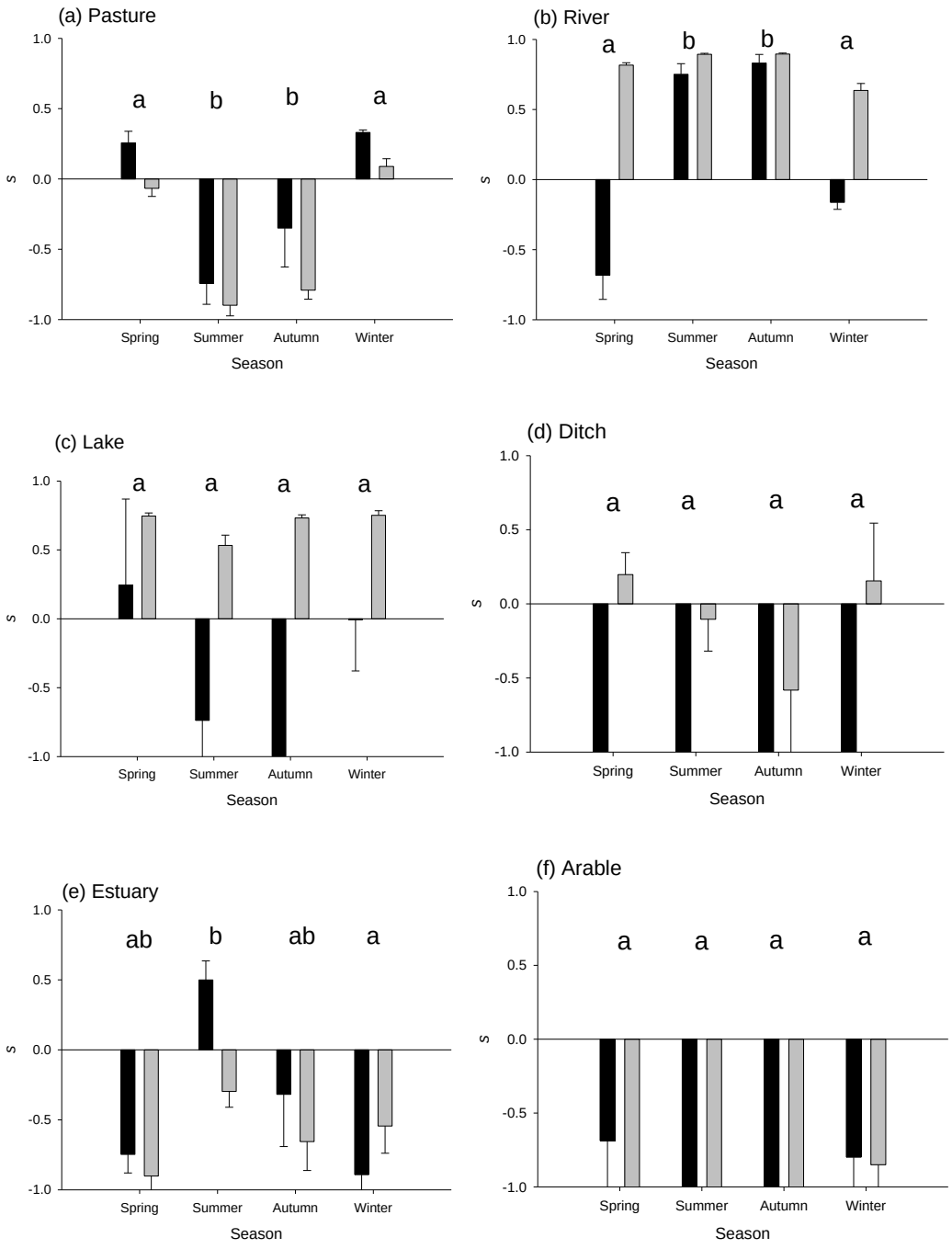


Figure 5.4: *Seasonal differences in mean (± SE) habitat electivity (s) of the flock (dark bars) and breeding (light bars) subpopulations, indicating habitat preference (positive values) or avoidance (negative values). Letters indicate significant differences between seasons.*

Table 5.2: *The influence of season and swan social group on the electivity values for six habitat categories, as illustrated by a linear mixed effects model. Test statistics are* F *values for subject parameters (season, social grouping), and* t *values for within-subject parameters* [a] *This parameter has a value of zero as other parameters are relative to it.*

Habitat	Parameter	Coefficient	Coefficient SE	Test statistic	d.f.	*p*
Pasture	Season	-	-	41.05	27	< 0.001
	(Spring)	-0.13	0.12	-1.08	27	0.288
	(Summer)	-1.00	0.10	-9.72	27	< 0.001
	(Autumn)	-0.79	0.12	-6.53	27	< 0.001
	(Winter)	0.00 [a]	0.00	-	-	-
	Social group	-	-	15.72	27	< 0.001
	Flocks	0.32	0.08	3.97	27	< 0.001
	Breeders	0.00 [a]	0.00	-	-	-
River	Season	-	-	18.73	27	< 0.001
	(Spring)	-0.03	0.13	-0.25	27	0.808
	(Summer)	0.58	0.11	5.48	27	< 0.001
	(Autumn)	0.65	0.13	5.21	27	< 0.001
	(Winter)	0.00 [a]	0.00	-	-	-
	Social group	-	-	30.80	27	< 0.001
	Flocks	-0.45	0.08	-5.55	27	< 0.001
	Breeders	0.00 [a]	0.00	-	-	-
Lake	Season	-	-	3.17	27	0.041
	(Spring)	0.17	0.20	0.84	27	0.406
	(Summer)	-0.32	0.17	-1.91	27	0.067
	(Autumn)	-0.30	0.20	-1.55	27	0.133
	(Winter)	0.00 [a]	0.00	-	-	-
	Social group	-	-	27.74	27	< 0.001
	Flocks	-0.68	0.13	-5.27	27	< 0.001
	Breeders	0.00 [a]	0.00	-	-	-
Ditch	Season	-	-	1.25	27	0.310
	(Spring)	-0.08	0.19	-0.42	27	0.675
	(Summer)	-0.19	0.16	-1.15	27	0.260
	(Autumn)	-0.36	0.19	-1.85	27	0.076
	(Winter)	0.00 [a]	0.00	-	-	-
	Social group	-	-	30.43	27	< 0.001
	Flocks	-0.70	0.13	-5.52	27	< 0.001
	Breeders	0.00 [a]	0.00	-	-	-
Estuary	Season	-	-	9.17	27	< 0.001
	(Spring)	-0.06	0.17	-0.38	27	0.707
	(Summer)	0.61	0.14	4.26	27	< 0.001
	(Autumn)	0.15	0.17	0.86	27	0.399
	(Winter)	0.00 [a]	0.00	-	-	-
	Social group	-	-	6.15	27	0.020
	Flocks	0.28	0.11	2.48	27	0.020
	Breeders	0.00 [a]	0.00	-	-	-
Arable	Season	-	-	1.28	27	0.301
	(Spring)	0.05	0.18	0.26	27	0.795
	(Summer)	-0.21	0.15	-1.38	27	0.178
	(Autumn)	-0.21	0.18	-1.17	27	0.252
	(Winter)	0.00 [a]	0.00	-	-	-
	Social group	-	-	0.98	27	0.331

Flocks	0.12	0.12	0.99	27	0.331
Breeders	0.00 [a]	0.00	-	-	-

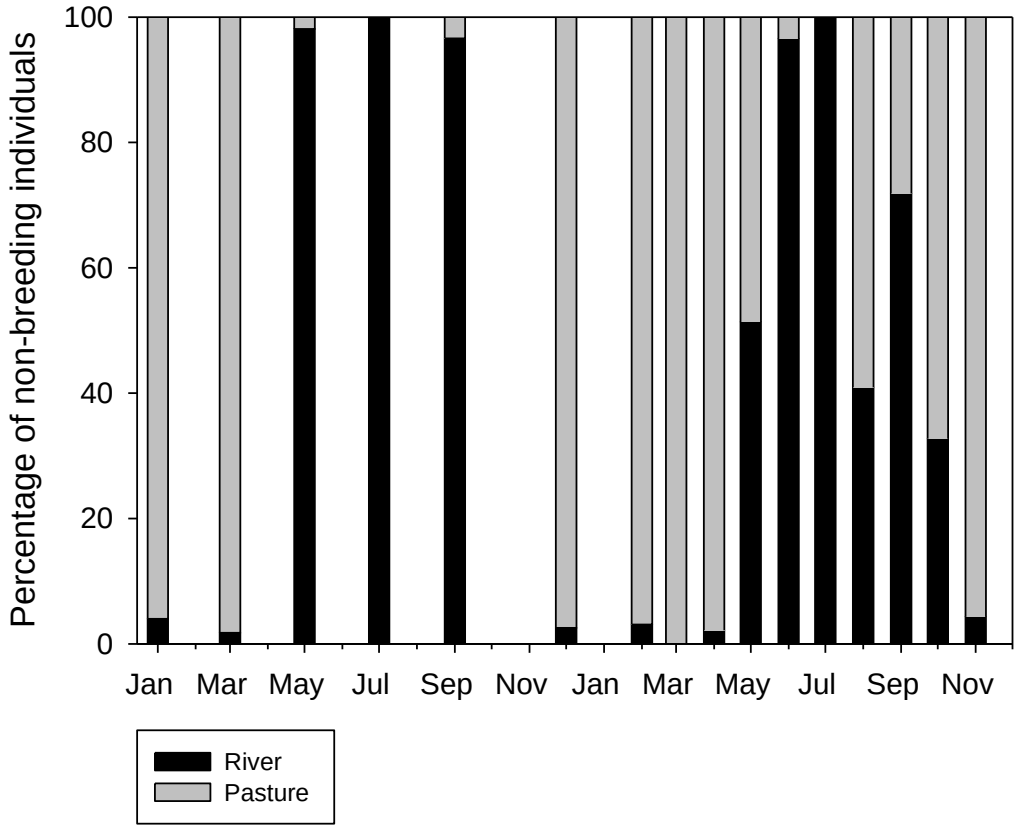


Figure 5.5: *The temporal pattern in the relative distribution of non-breeding swans between river and pasture habitat over a two year period, indicating the timing of the switch between habitats.*

5.5 Discussion

In this study I used data from repeated surveys of the swan population of a chalk river catchment to quantify spatiotemporal patterns of swan population structure, reproduction and habitat use. Data on the social, age and sex ratios, as well as breeding population size and productivity and habitat preferences have previously been lacking for chalk river catchments, in which swan grazing conflicts have been reported. Such data are required to facilitate the construction and testing of field experiments and ecological models that evaluate different strategies which attempt to alleviate swan grazing conflicts.

5.5.1 Structure

I found that the swan population was dominated by flocks, with smaller proportions of breeding birds and few swans observed alone, in common with previous studies of swan populations (Minton, 1971; Coleman *et al*., 2001). However, the sizes of all social groups changed over seasons, indicating that models of swan grazing conflicts must be temporally explicit and account for seasonal changes in grazing pressure. The mean flock size remained relatively constant across seasons; the winter influx of swans to flocks resulted in the establishment of additional flocks rather than increasing the size of existing flocks. Given that flocks but not other social groups are associated with grazing conflicts (Trump *et al*., 1994; O'Hare *et al*., 2007), the presence of more flocks in winter could imply a greater potential for grazing conflicts in winter. However, in assessing the risk of grazing conflicts the densities, as well as the number, of the flocks should also be considered. In pasture fields swans can distribute themselves over a larger area, as fields are relatively open habitats free of obstructions, and thus the grazing pressure on any given area will be reduced (Harrison, 1985; Parrott & McKay, 2001a). By contrast in rivers the dispersal of swans in a flock is limited by the narrow river channel (typically < 15 m) and the presence of territorial pairs upstream and downstream; thus given that mean flock size did not vary in this study, the densities in rivers is likely to be higher than in pasture fields. Both the total population and flock subpopulations were mostly comprised of adult birds; the dominance of heavier-bodied adults has perhaps given rise to a greater grazing conflict than if flocks were dominated by lighter juveniles (**Chapter 2**). Typical adult mass is 10.8 kg compared with 8.8 kg for a juvenile, thus unless flock densities are high the mass difference between equal numbers of adults and juveniles will be small (Delany, 2005). According to the relationship between waterfowl biomass density and reductions in plant biomass derived in **Chapter 2**, the reduction in plant biomass associated with an all-adult flock would be only 2.1 % greater than that observed for the same numerical density of juveniles, due to the small increase in reduction in plant biomass observed for every kilogram per hectare increase in herbivore biomass density.

The population sex ratio was close to parity; typically in avian populations higher mortality in females yields a sex ratio skewed towards males (Donald, 2007). The balanced sex ratio observed in the Frome population may therefore be the result of the high (> 70 %) survival rates reported for chalk river swans (Trump *et al.*, 1994; Watola *et al.*, 2003). Whilst my data were collected over different seasons, previous research suggests that the sex ratios of mute swan populations are stable throughout the year (Coleman *et al*., 2002).

5.5.2 Reproduction

The number of swans that bred was low given the large number of birds of breeding age observed within the catchment. The two key limiting steps appeared to be pair formation and territory establishment; only 48.9 % of individuals of breeding age had formed a pair, and only 69.6 % of paired individuals successfully established a territory. Mute swan pair formation and territory establishment are typically independent, with most pair formations occurring whilst the individuals live within non-territorial flocks (Minton, 1971; Coleman *et al*., 2001). As some non-territorial pairs live within flocks I may have underestimated the true number of paired individuals within the catchment (Minton, 1971). However, strong competition for territories appeared to limit the number of pairs that could breed successfully. The breeding density on the River Frome, of 1 pair per 2.45 km of river, is slightly lower than the 1 pair per 1.75 km and 1.48 km reported by Trump *et al*. (1994) for two other chalk rivers, the River Wylye and River Avon respectively. Mean clutch size per nest in the River Frome (4.4) was lower than that reported for another chalk river, the River Wylye (6.3), where illegal clutch reductions were believed to have occurred, which suggests that such reductions may be less prevalent than originally suspected (Trump *et al*., 1994; Watola *et al*., 2003). The lower productivity and lower breeding density observed may indicate that the River Frome represents inferior breeding habitat relative to the River Wylye. Whilst both rivers have similar abundances of the same plant communities dominated by water crowfoot, there may be differences in plant nutritional quality, hydrology, channel morphology, predator densities or other unknown factors (Trump *et al*., 1994; O'Hare *et al*., 2007).

5.5.3 Habitat use

A clear seasonal switch in habitat use was observed, with pasture preferred in spring and winter and river preferred in summer and autumn. Habitat availability was constant between seasons, but the relative quality and thus profitability of these habitats probably varied with season. In particular, the river appears to be most preferred during the period of the lowest river flow and turbidity and highest aquatic plant biomass (O'Hare *et al*., 2007). In contrast to some other swan populations (*e.g.* Chisholm & Spray, 2002) arable fields were typically avoided. This difference may be explained by the different patterns of land use in the different study areas; in particular the River Frome catchment lacked fields of Oilseed Rape (*Brassica napus* L.) which were a preferred habitat in the River Tweed catchment, Scotland (Chisholm & Spray, 2002). Patterns of habitat use may thus depend, at least in part, on the availability, quality and distribution of preferred food plants within the landscape.

I found different habitat preferences for flock and breeding individuals. Breeding individuals consistently preferred freshwater habitats, particularly river and lake habitat with ditches typically only preferred in winter. Freshwater habitats offer both abundant plant food and security for cygnets from terrestrial predators during the breeding period, making them attractive breeding habitats (Birkhead & Perrins, 1986). Breeding individuals continued to exhibit a preference for river habitat even during periods of high flow in winter, presumably because of the need to defend it from other pairs due to the strong competition for territories reported here and by Scott (1984). Flock individuals exhibited a preference for aquatic riverine habitat in summer and autumn, and for terrestrial pasture in winter and spring. As aquatic plant biomass is typically higher in summer and autumn than winter or spring (O'Hare *et al.*, 2007) the observed habitat switch may be due to seasonal changes in the profitability of pasture and riverine habitats; this should be investigated further as understanding how swans respond to changes in food availability could allow the design of sacrificial feeding areas to alleviate grazing conflicts in sensitive areas of plant habitat (Owen, 1977; Spray *et al*., 2002).

5.5.4 Implications for alleviating grazing conflicts

Attempts to manage the swan population, for example through translocation or culling, will be complicated by the seasonal variation in the population structure and seasonal movements of swans identified in my study. It will not be possible to manage the flock subpopulation without also affecting the breeding subpopulation, which may be controversial as only the flock subpopulation is known to cause grazing conflicts (Trump *et al*., 1994; O'Hare *et al*., 2007; **Chapter 4**). Removal of swans between spring and autumn will not prevent swan flocks grazing on pasture or crops in winter, as many of the swans present in the winter flocks spend the spring to autumn period outside of the catchment. Removal of swans in the Frome catchment in winter will remove resident and overwintering swans, which may have effects outside of the Frome catchment when overwintering swans do not return to their breeding or spring-autumn areas. Additionally, removal of swans or reductions in reproductive output within the catchment may be offset by immigration from other areas (Trump *et al*., 1994). Population models could be used to test the validity of these conclusions under different methods of population management. Any reduction in swan numbers must be judged against the high degree of controversy surrounding the idea of population control in mute swans in the UK, where swans are very popular with the public (Birkhead & Perrins, 1986; Kear, 1988; Sladen, 1991; Delany, 2005). Habitat management which focuses on protecting sensitive areas of plant habitat, rather than population control, may be a more effective means of alleviating conflicts with swans.

Chapter 6: Can mute swan population management alleviate a grazing conflict in a chalk river catchment? Insights from a mathematical model.

6.1 Abstract

Abundant herbivores can damage plants and so cause conflict with conservation, agricultural, and fisheries interests. Management of herbivore populations is a potential tool to alleviate such conflicts but may raise concerns about the economic and ethical costs of implementation, especially if the herbivores are 'charismatic' and popular with the public. Thus it is critical to evaluate the probability of achieving the desired ecological outcomes before proceeding to a field trial. In this study I assessed the potential for population management to resolve a conflict of non-breeding swans grazing in chalk river catchments. I used an age-structured mathematical model to evaluate the consequences of three population management strategies; (a) reductions in reproductive success, (b) removal of individuals, and (c) reduced reproductive success and removal of individuals combined. A comparison of stochastic and deterministic models found that the stochastic model most accurately predicted observed historical changes in the sizes of two chalk river swan populations. Only reducing reproductive success to 0 every year, or combining substantial reductions in reproductive effort and annual removal, reduced the population below the level for which grazing conflicts have been previously reported. These high levels of management effort will be difficult to achieve and maintain, thus such strategies are unlikely to alleviate swan grazing conflicts alone or in combination. Additionally, such management would likely prove financially and ethically problematic. Predictions of population responses to management were affected by survival rate, productivity and immigration. Grazing conflicts with large charismatic herbivores, such as waterfowl and ungulates, are increasing and effective management is required to alleviate ecological and socioeconomic damage. This study has demonstrated that mathematical population models can be an accurate, cost-effective method of evaluating the consequences of different management strategies.

6.2 Introduction

How to manage species and environments for the benefits of conservation, economic, and human well-being objectives is a central challenge facing society (Sutherland *et al*., 2009). Such management can often involve population reductions; humans intervene to reduce population size in a range of species, for example to eradicate invasive species

and limit the population of agricultural pests (Wright & Phillips, 1991; Ellis & Elphick, 2007; Williams *et al*., 2007). Population control typically focuses on reducing the number of individuals through translocation (Hodder & Bullock, 1997; Duka & Masters, 2005) or culling (Murton *et al*., 1974; Middleton *et al*., 1993; Smith *et al*., 2008), or on reducing reproductive output through fertility control (Brooks *et al*., 1980; Duka & Masters, 2005; Williams *et al*., 2007) or, in birds, destroying eggs (Wright & Phillips, 1991; Baker *et al*., 1993; Watola *et al*., 2003). Selecting appropriate methods of population control requires consideration of the ecological, economic, and ethical consequences of control (Duka & Masters, 2005; Minteer & Collins, 2005; Ellis & Elphick, 2007). Aside from the financial costs of management, which can be great, the manipulation of animal populations can also be an emotive issue, particularly where lethal methods are used or target species are charismatic (Sladen, 1991; Perry & Perry, 2008). Thus managers must ensure that methods of population control are likely to achieve the desired ecological outcomes, are cost effective, and are conducted in the most ethical manner possible.

Large vertebrate herbivores can damage vegetation of ecological and socioeconomic value through consumption, trampling and altered nutrient concentrations (Milchunas & Lauenroth, 1993; Côté *et al*., 2004; **Chapter 2**). Such damage may require management to alleviate the effects of herbivory and protect either the plants or other organisms that depend on such plants (Watola *et al*., 2003; Duka & Masters, 2005; Ellis & Elphick, 2007; Williams *et al*., 2007). Mute swans (*Cygnus olor* Gmelin, 1789) are charismatic herbivores known to reduce plant abundances in both aquatic and terrestrial habitats Harrison, 1985; Parrott & McKay, 2001a; O'Hare *et al*., 2007; **Chapter 4**). Recent studies have reported that swan flocks can cause substantial reductions in aquatic plant abundance in the chalk rivers of southern England (O'Hare *et al*., 2007; **Chapter 4**); such plants are protected under the EU Habitats and Species Directive (92/43/EEC) due to the abundant and diverse biota that are supported. Swan herbivory also occurs in pasture fields adjacent to chalk rivers; a mean pasture grass yield loss of 11.4 % in fields grazed by flocks of swans has been reported, which increased livestock feeding costs for the farmers affected (Harrison, 1985). Thus a conflict exists in chalk river catchments between a protected charismatic herbivore species and the protected, high-value plants that are damaged. Reducing the number of swans in areas of conflict through population management has been suggested as a means to alleviate swan grazing conflicts (Trump *et al*., 1994). However, recent culls of mute swan and black swan (*Cygnus atratus* Latham, 1790) populations in the United States and New Zealand respectively faced widespread public opposition, legal challenges, and damaged relations between different stakeholder groups, in particular government wildlife officials, landowners and animal welfare groups (Minteer & Collins, 2005; Perry & Perry, 2008). A major point of contention between these stakeholders was whether the proposed methods of population control were the most effective means of alleviating herbivore damage (Sladen, 1991; Perry &

Perry, 2008). In general, the manipulation of clutch sizes is considered the least ethically controversial method, and combined removal of birds and clutch control is likely to attract most opposition. Therefore the range of available population management methods represent a wide range in terms of costs, ethics, and crucially, ecological outcomes. Thus evaluations of the probabilities of different methods of population control achieving their desired ecological outcomes, in a cost-effective and ethical manner, should be conducted prior to field trials to minimise the rancour experienced during the schemes in the US and New Zealand.

Mathematical models allow the prediction and evaluation of the consequences of management decisions on species abundances and distributions (*e.g.* Middleton *et al*., 1993). In this paper I developed a mathematical model to evaluate the consequences of different management strategies on a swan population at the scale of a river catchment. I built on previous research by constructing and testing deterministic and stochastic mathematical models of a mute swan population in a chalk river catchment (Watola *et al*., 2003; Ellis & Elphick, 2007). Watola *et al*. (2003) used a small-scale (16.9 km river length) deterministic model to predict the population-level outcomes of reducing reproductive output through the destruction of eggs in a UK chalk river swan population; however, as this model was deterministic the uncertainty surrounding such outcomes was not quantified. Additionally, the small-scale may preclude accurate predictions of the numerical responses of swan populations to management; swans exhibit seasonal movements between different habitats within a river catchment, thus a more appropriate scale may be the catchment-scale (**Chapter 5**). Ellis & Elphick (2007) used a stochastic model to inform the eradication of an invasive mute swan population in North America. However, the potential differences in demography between a rapidly-expanding invasive population and a population within its natural range, as well as the different management objectives, mean that a new model is required to test the range of proposed management strategies for chalk river swan populations. Breeding swans are highly territorial, excluding other individuals from a given area, which is a key factor regulating mute swan population dynamics (Birkhead & Perrins, 1986; Trump *et al*., 1994; **Chapter 5**); however, territoriality has not been incorporated into previous swan population models.

A criticism of deterministic population models, which utilise mean values for population parameters and thus focus on mean population outcomes, is that such models do not incorporate the demographic or environmental uncertainty documented for natural populations (Jagers, 2010). Consequently, deterministic models may not accurately predict population responses observed in nature, nor provide managers with estimates of the uncertainties regarding the population outcomes of specific management decisions.

Conversely, complex stochastic models may yield predictions associated with large margins of error and numerous caveats which are not useful to managers. Scientists must balance the need to provide managers with simple, accurate predictions of population responses with the need to provide estimates of error associated with that prediction. The choice of model should reflect this balance.

In this study I first tested the ability of a stochastic and a deterministic model to generate accurate predictions of historical changes in population size for two different chalk river swan populations. I then used the most accurate of my stochastic and deterministic models to predict the population-level responses over time to (a) the removal of adult or juvenile swans, simulating the effects of translocation or culling, (b) reductions in reproductive output, simulating the effects of fertility control or egg destruction, and (c) the combined effects of (a) and (b). Previous research has demonstrated that single applications of a population control (*i.e.* carried out in one year only) on established, open populations of long-lived animals capable of rapid dispersal is seldom effective, with rapid (< 5 years) recovery from any reductions (Middleton *et al*., 1993; Trump *et al*., 1994; Vickery *et al*., 1994). Thus I tested the effects of repeated annual population control sustained over time. Swans are known to immigrate into chalk rivers from marginal habitats, such as farm ponds, outside the catchment, although the number of immigrants likely varies considerably between different chalk rivers (Trump *et al*., 1994; Watola *et al*., 2003; **Chapter 5**). To allow the model to make general predictions across different chalk river catchments I tested the population-level responses to management in both an open, *i.e.* with immigration, and a closed system, *i.e.* without immigration. Additionally, I examined the effects of varying the numbers of immigrants on the model predictions. Whilst closed populations are atypical in mute swans (Birkhead & Perrins, 1986; but see McCleery *et al*., 2002), they are more common in other grazing waterfowl species (Owen & Norderhaug, 1977; Middleton *et al*., 1993). Thus this study represents the most comprehensive assessment to date of the potential of different methods of population management to alleviate swan grazing conflicts in chalk rivers.

6.3 Methods

6.3.1 Study system

The River Frome (Dorset, UK) is a shallow, mesotrophic chalk river that flows through a catchment dominated by mixed pastoral and arable agriculture. The model was constructed for the 68.5 km length of the River Frome catchment described in **Chapter 5**. The catchment has a mean population of 298 swans, which exhibit seasonal movements between riverine (summer-autumn) and pastoral (winter-spring) habitats within the

catchment (**Chapter 5**). Complaints of grazing damage in the River Frome catchment began after the year 1996 (Ilsington Angling Club & Moreton Estate, personal communications). Thus reducing the swan population to pre-1996 levels may alleviate the grazing conflict. Whilst historical data for the entire River Frome catchment is lacking, surveys of the lower 19.4 km of the catchment in 1995 reported a population size of 73 individuals (Liley *et al*., 2008). Based on the 16 recent total catchment surveys reported in **Chapter 5**, the lower 19.4 km accounts for a mean (± 95 % CI) of 47 ± 5 % of the total catchment population. Thus in 1995 the total catchment population was estimated at 155 ± 14 individuals.

6.3.2 Population model

I constructed two age-structured mathematical population models with a twelve month time step (*i.e.* projection interval); a deterministic model with fixed (mean) parameters and a stochastic model with parameters which could vary between years. In each time step of the stochastic model, parameter values were selected from a normal error distribution from the data range (mean ± SD) for a given parameter. The deterministic model used the mean value for each parameter. The two models were otherwise identical. Model parameters were derived from data presented in studies of chalk river swan populations (**Table 6.1**). The models consisted of three age classes of swan; cygnets, juveniles and adults. Adult swans were further subdivided into breeding and non-breeding adults based on territory availability; adults were defined as breeding if they were randomly allocated one of the fixed number of territories. I based the initial demographic distribution (*i.e.* relative numbers of adults, juveniles and cygnets) on the mean (± SD) September counts given in **Chapter 5**. The model time step ran from October to September, as September is typically the month in which cygnets fledge and become juveniles, and begin to leave their natal territory (Birkhead & Perrins, 1986; **Chapter 5**).

***Table 6.1**: Population model parameter mean values and standard deviations; see text for derivation. * The upper limit for breeding adult survival rate was set to 1.00, as survival cannot exceed this threshold.*

Parameter	Mean	SD	Reference
Initial number of adults (*A*)	147	± 2.83	Chapter 5
Initial number of juveniles (*J*)	52	± 31.11	Chapter 5
Initial number of cygnets (*C*)	58	± 9.19	Chapter 5
Number of breeding territories (*T*)	38	± 9.24	Trump *et al*. (1994); Chapter 5
Number of eggs per breeding adult (*E*)	2.20	± 2.80	Chapter 5
Breeding adult survival rate ($_sB$)	0.90	± 0.11	Watola *et al*. (2003) *
Non-breeding adult survival rate ($_sN$)	0.71	± 0.23	Watola *et al*. (2003)
Juvenile survival rate ($_sJ$)	0.73	± 0.25	Watola *et al*. (2003)
Cygnet survival rate ($_sC$)	0.37	± 0.36	Chapter 5
Number of adult immigrants ($_iN$)	43.2	± 17.81	Watola *et al*. (2003); Chapter 5
Number of juvenile immigrants ($_iJ$)	6.9	± 2.74	Watola *et al*. (2003); Chapter 5

I calculated the total swan population *P* for the year $_t$ as:

$P_t = C_t + J_t + A_t$,

where, *C*, *J*, and *A* were the sizes of the cygnet, juvenile, and adult subpopulations respectively.

C_t was estimated as:

$C_t = (E \cdot B_t) \cdot {}_sC$,

J_t was estimated as:

$J_t = (C_{t-1} + {}_iJ) \cdot {}_sJ$,

and A_t was estimated as:

$A_t = ((J_{t-1} + N_{t-1} + {}_iN_t) \cdot {}_sN) + (B_{t-1} \cdot {}_sB)$,

where, N and B were the sizes of the non-breeding adult and breeding adult subpopulations respectively. ${}_sC$, ${}_sJ$, ${}_sN$, and ${}_sB$ were the annual survival rate of cygnets, juveniles, non-breeding adults and breeding adults respectively. Juvenile and adult survival rates, as estimated by Watola *et al*. (2003), represented the probability of an individual not leaving the study area either through death or emigration, and as such represent 'apparent survival'. E was the annual number of eggs produced per breeding adult. ${}_iJ$ and ${}_iN$ were the numbers of annual immigrant juveniles and non-breeding adults respectively. No cygnet immigration was permitted in the models as swans do not typically leave their natal territory until at least seven months old, *i.e.* until they have become juveniles (Birkhead & Perrins, 1986). In chalk river swan populations immigration occurs as birds fledged on waterbodies away from the river join the flocks on the river or adjacent pasture fields (Trump *et al*., 1994; **Chapter 5**). Thus the number of immigrants was assumed to be proportional to the length of the river, *i.e.* a longer section of river should receive more immigrants as it has a larger surrounding area to supply such immigrants. Watola *et al*. (2003) estimated that the mean annual numbers of juvenile and adult immigrants to a 16.9 km length of chalk river were 1.66 ± 0.73 SD and 10.58 ± 4.44 SD respectively, indicating 0.10 ± 0.04 juveniles and 0.63 ± 0.26 adult immigrants per km of river length. Thus the 68.5 km river length of River Frome in this study was assumed to receive 6.9 ± 2.7 juvenile and 43.2 ± 17.8 adult immigrants per year. Such values were within the seasonal variation in the River Frome swan population size (**Chapter 5**).

A_t was subdivided into N_t and B_t depending on the number of adult individuals and the availability of breeding territories, according to:

B_t = if ($A_t \geq (2T)$, $(2T)$, A_t),

N_t = if ($A_t \geq B_t$, $A_t - B_t$, 0),

where T is the number of breeding territories available. I estimated T as 38 ± 9.24, after the mean densities of breeding pairs per length of chalk river reported by (Trump *et al*., 1994; **Chapter 5**).

The models ran over a 50 year period, which allowed time for model properties to emerge whilst also being a time scale relevant to managers (Ellis & Elphick, 2007). Model simulations were run in Python 3.1 (Python Software Foundation) from a parameter file (**Appendix 4**). Simulations were run 1000 times for each management strategy, from which I quantified the predicted stable population size, measured as the mean (± 95 % CI) predicted population size between year 36 and 50.

6.3.3 Model validation

To test the accuracy of the predictions of our stochastic and deterministic models, I compared model predictions with historical population data for the swan populations of a 34.8 km section of the River Wylye (Trump *et al*., 1994) and a 19.4 km section of the River Frome (Liley *et al*., 2008). Historical data for both populations spanned 16-year periods, although the time series for the River Frome was incomplete.

6.3.4 Sensitivity analysis

I assessed the sensitivity of the predicted population size to changes in the mean value of each parameter in two ways, following the the one-at-a-time method of local sensitivity analysis (Hamby, 1994). Firstly, to examine the uncertainty in model predictions associated with the variance of each parameter, I subjected each parameter in turn to (a) an increase of 1 SD and (b) a decrease of 1 SD. Secondly, to examine which parameters had the greatest relative effect on model predictions, I subjected each parameter in turn to (a) an increase of 25 % and (b) a decrease of 25 %. As I was interested in the population outcomes predicted by the model I compared the effects of parameter value changes on the predicted stable population size.

6.3.5 Management strategies tested

I tested three management strategies; (a) the effects of manipulating reproductive success, (b) the effects of removing a given percentage (*R*) of the non-breeding subpopulation, and (c) the combined effects of (a) and (b), on the predicted swan population size. The non-breeding subpopulation was targeted as grazing conflicts have been reported for these, but not breeding, individuals and thus removal of breeding birds is likely to prove unacceptable to stakeholders (Sladen, 1991; Trump *et al*., 1994; O'Hare *et al*., 2007; Perry & Perry, 2008). I used the number of eggs per nest, or 'clutch size' (2*E*) as the estimate of reproductive success. Clutch sizes between 0 and 10 eggs per nest were tested, covering the range of clutch sizes reported for mute swans (Birkhead & Perrins, 1986). The non-breeding subpopulation was the sum of the non-breeding adults and juveniles; I tested values of *R* at 5 % increments between 0 and 100 % inclusive in order to test the full range of options. In the stochastic model, when varying *E* and *R*, I set the standard deviation of those parameters to zero, but all other parameters were allowed to vary.

6.4 Results

6.4.1 Model validation

Relative to the deterministic model, the population sizes predicted by the stochastic model were closer to the historical data available for both chalk rivers. The population sizes predicted by the stochastic model, as a mean (± 95 % CI) percentage of the observed population sizes, were 97.9 ± 8.4 % for the River Wylye population compared with 83.5 ± 7.7 % for the deterministic model (**Figure 6.1a**). For the River Frome population in the earlier years the deterministic model was slightly closer to the observed, however, in the later years the mean predictions of the stochastic model were closer (**Figure 6.1b**). Over the entire period, the mean predictions of the stochastic model were 107.0 ± 18.6 % for the River Frome population compared with 92.0 ± 19.4 % for the deterministic model. Thus I found generally close agreement between the stochastic model predictions and actual population sizes. The tendency of the deterministic model to underestimate observed population size presented a risk of providing erroneous management advice; the deterministic model could have given a false positive by indicating that a management option could have successfully reduced population size below the threshold when it actually could not. Observed population sizes were well within the 95 % confidence intervals predicted by the stochastic model for all years for both populations, although these confidence intervals were large due to both the number of parameters and the amount of natural variability around the mean (**Table 6.1**). As the more accurate, and less likely to underestimate, of the two models tested, the stochastic model was used to assess model sensitivity and further predict population changes in response to the three management scenarios.

6.4.2 Sensitivity analysis

The stochastic model was most sensitive to variance in the survival rate of the non-breeding adult swans, which comprised the majority of the swan population (**Figure 6.2a**). Varying parameters by ± 25 % indicated that the stable population size predicted by the stochastic model was affected most strongly by changes in the survival rate of non-breeding adults, with some, albeit lower, effects of the survival rates of breeding adults, juveniles and cygnets, as well as breeding and immigration parameters (**Figure 6.2b**). The stable population size was not affected by altering the initial numbers of adults, juveniles and cygnets.

6.4.3 Population management

The model predicted a mean stable population size of 469 individuals (95 % CI = 207 to 881) if no management action were taken. However, removing all eggs within the catchment each year (*i.e.* 0 eggs per nest) was predicted to yield a stable population size of 153 individuals (95 % CI = 89.6 to 239.7), marginally below the target population threshold of 155 (**Figure 6.3a**). Removing 100 % of the non-breeding subpopulation (*i.e.* juveniles and non-breeding adults) annually was predicted to results in a stable population sizes of 191 ± individuals (95 % CI = 72 to 458), in excess of the 155 individuals target (**Figure 6.3b**). The combined effects of reduced reproductive success and removal of individuals could reduce the population below the target, but required either very low reproductive success, large removals of individuals, or both to be successful (**Figure 6.3c**).

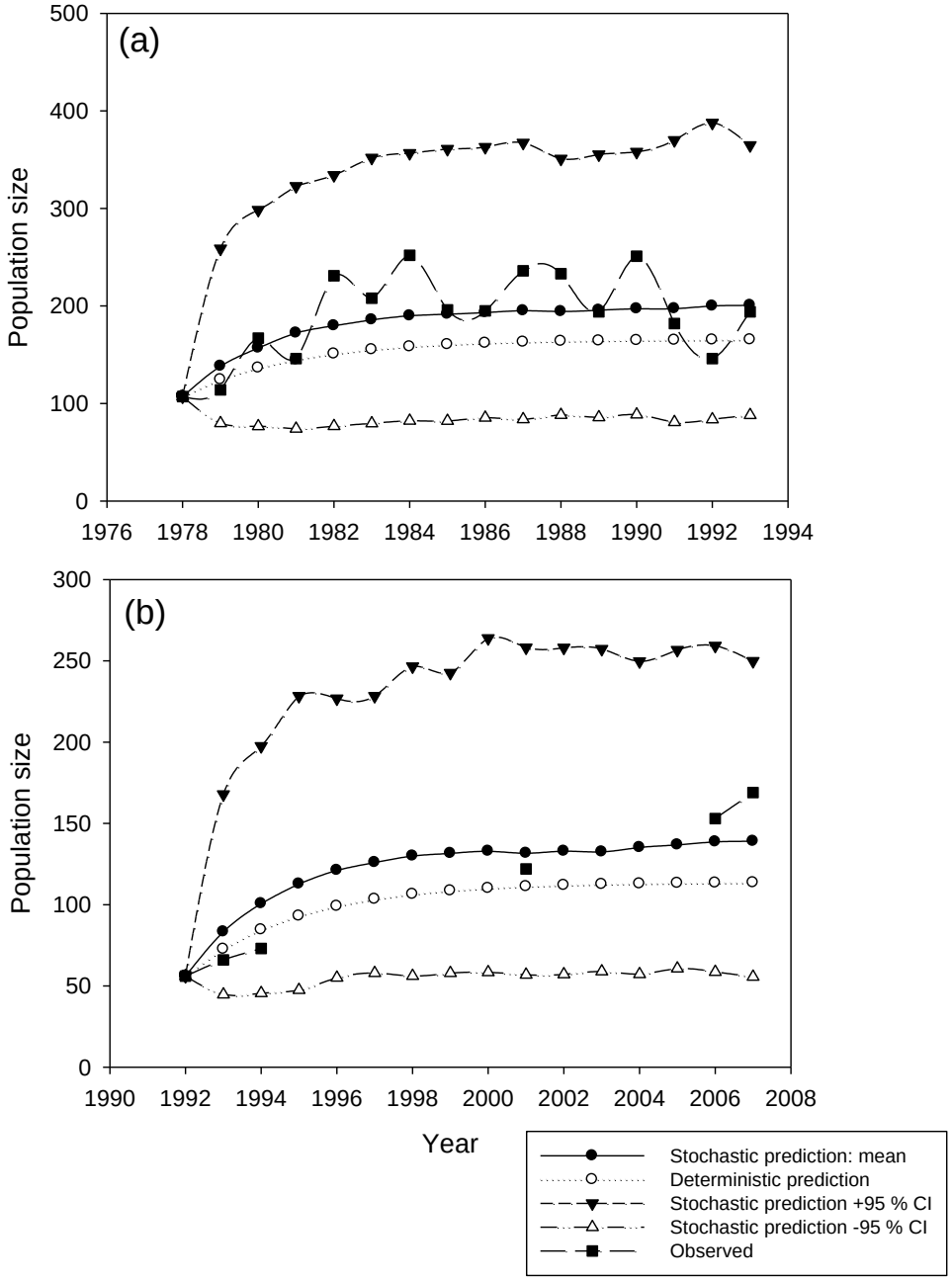


Figure 6.1: *Comparisons between observed historical data and mean (± 95 % CI) stochastic and deterministic model predictions of the swan populations in (a) the River Wylye and (b) the River Frome.*

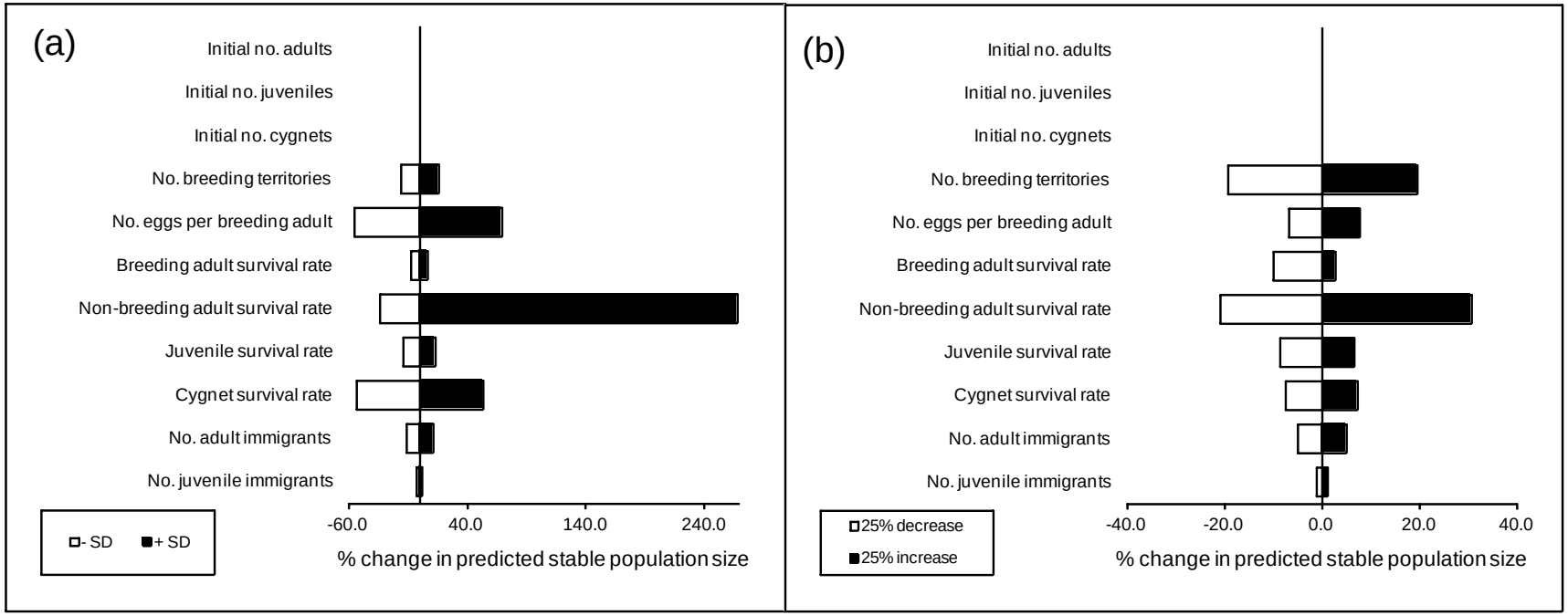
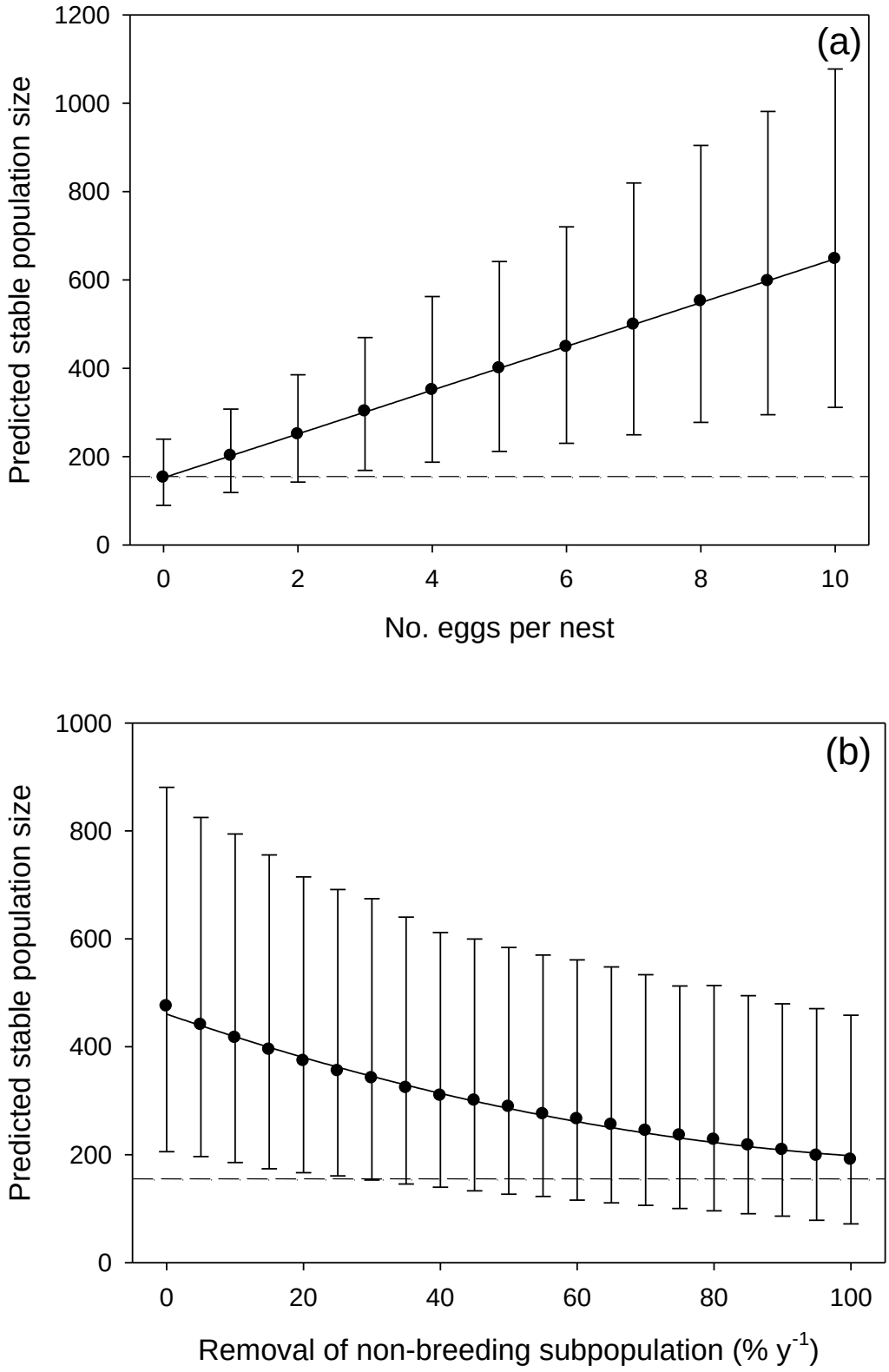


Figure 6.2: *The sensitivity of the model predictions to (a) ± 1 SD and (b) ± 25 % changes in the mean value of each parameter.*


(a)
Predicted stable population size
1200
1000
800
600
400
200
0
0
2
4
6
8
10
No. eggs per nest
(b)
Predicted stable population size
1000
800
600
400
200
0
0
20
40
60
80
100
Removal of non-breeding subpopulation (% y-1)

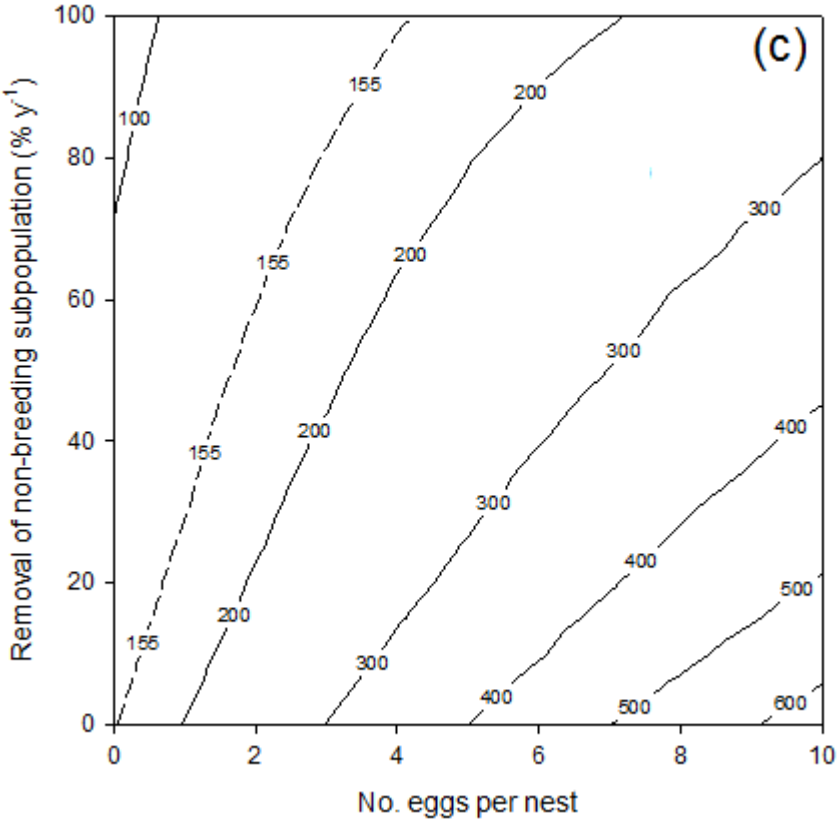


Figure 6.3: *The effects on the mean (± 95 % CI) predicted stable population of changes to (a) the reproductive output (clutch size 2E), (b) the annual percentage of the non-breeding subpopulation removed (R), and (c) both the reproductive output and annual percentage of non-breeders removed. The target population size of 155 individuals is indicated by the dashed line.*

Population reductions through reduced reproductive success and the removal of non-breeding individuals were predicted to be offset by immigration from outside of the catchment. The percentage change in predicted stable population size was positively related to percentage changes in the number of immigrant swans (**Figure 6.4**).

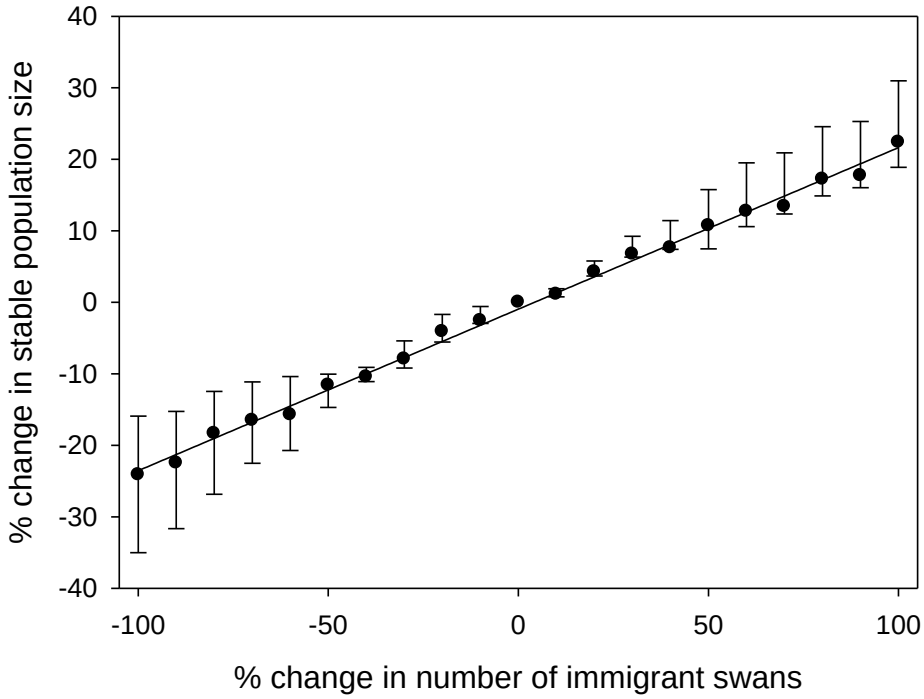
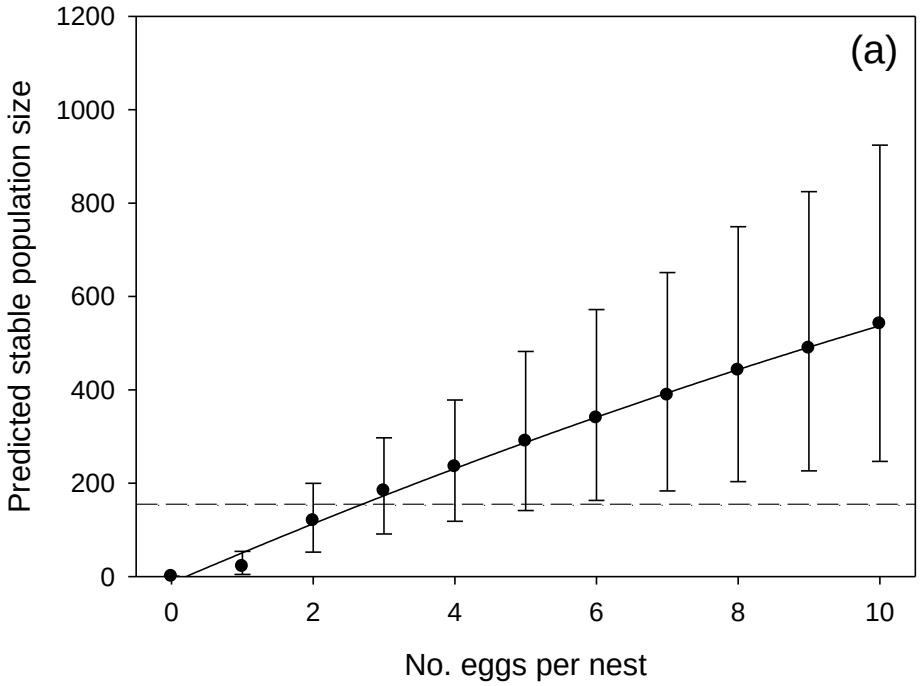
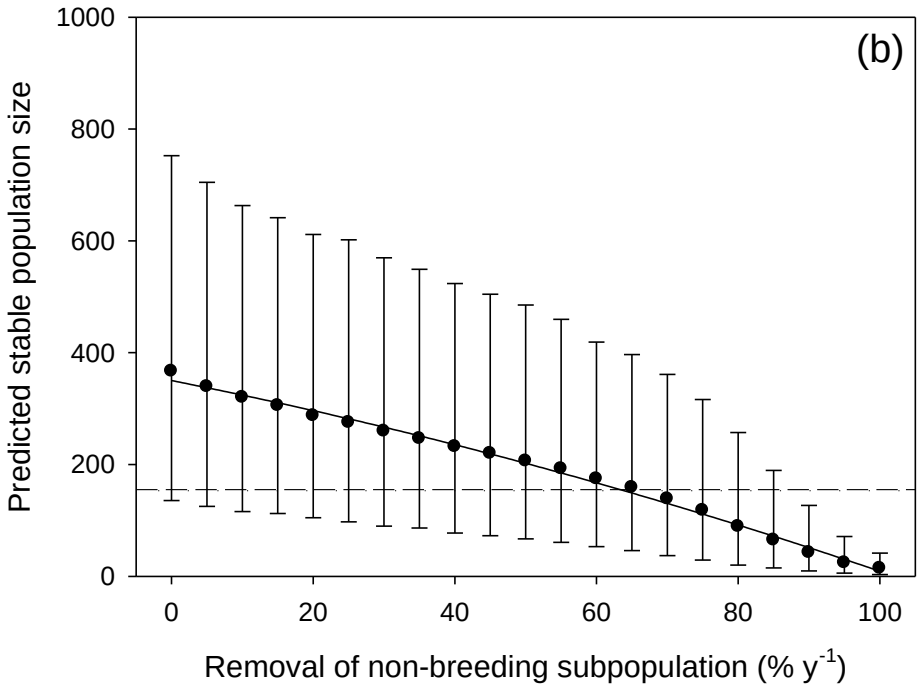


Figure 6.4: *The effects of percentage changes in the number of immigrant swans on the stable population size predicted by the model.*

In a closed system (*i.e.* without immigration) removing all eggs per nest each year led to a stable population size of 0 individuals, *i.e.* the population reached extinction by year 39. The stable population size was predicted to be below the 155 target for a mean of ≤ 2.7 eggs per nest (**Figure 5a**). Similarly, in a closed system removing 100 % of the non-breeding population per annum was predicted to yield a stable population size of 0 individuals *i.e.* the population reached extinction by year 41. The stable population size was predicted to be below the 155 target for a mean annual reduction of ≥ 64 % (**Figure 5b**). Again, combining the removals of eggs and individual swans was the most effective of the three strategies in reducing the population below the target (**Figure 5c**).


(a)
Predicted stable population size
1200
1000
800
600
400
200
0
0
2
4
6
8
10
No. eggs per nest


(b)
Predicted stable population size
1000
800
600
400
200
0
0
20
40
60
80
100
Removal of non-breeding subpopulation (% y-1)

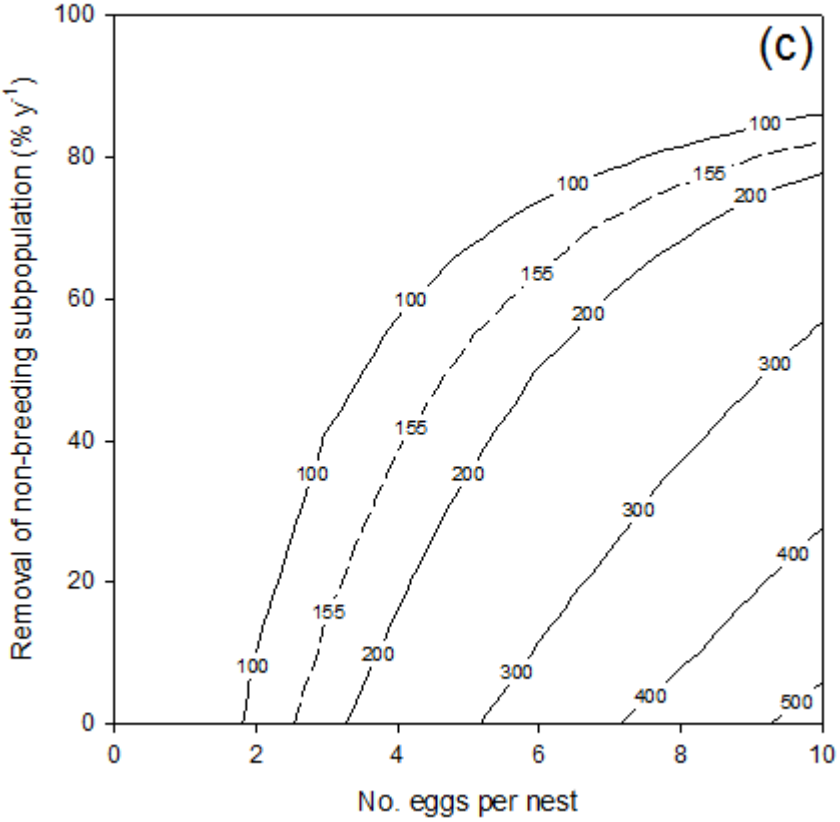


Figure 6.5: *The effects on the mean predicted stable population of changes in the absence of immigration to the (a) reproductive output (2E), (b) annual percentage of the non-breeding subpopulation removed (R), and (c) both the reproductive output and annual percentage of non-breeders removed. The target population size of 155 individuals is indicated by the dashed line.*

6.5 Discussion

In this study I constructed and tested stochastic and deterministic mathematical models of mute swan populations causing conflicts with agricultural, fisheries and conservation interests. The models built and improved on previous swan population models by assessing management at the catchment-scale and by incorporating territoriality, which is a key factor regulating mute swan population dynamics (Birkhead & Perrins, 1986; Trump *et al*., 1994; **Chapter 5**). Thus this study represents the most comprehensive assessment to date of the potential of different methods of population management to alleviate swan grazing conflicts in chalk rivers. The stochastic model more accurately predicted historical changes in the observed population sizes of two chalk rivers, therefore I used this model to predict the outcomes of attempts to alleviate grazing conflicts through reductions in the swan population by (a) reducing reproductive success, (b) removing non-breeding individuals, and (c) the combined effects of (a) and (b). As such, my study quantified the relationships between different management strategies and the strength of the corresponding population response. Grazing conflicts with large charismatic herbivores, such as ungulates and waterfowl, are increasing and effective management is required to alleviate ecological and socioeconomic damage (Côté *et al*., 2004; **Chapter 2**). Given the high costs and ethical issues associated with the implementation of population control measures, the arguments for or against a particular measure can be strengthened if the chances of success can be evaluated prior to field trials. This study has shown how mathematical population models can accurately predict population trends, and be a cost-effective method of evaluating the suitability of different management strategies.

For both chalk river swan populations tested, the stochastic model generated mean predictions of the changes in population size which were close to observed, historical data. Although these historical data sets represent smaller areas and shorter time scales than I used in the management simulations no other data were available for chalk river populations. Thus the models were validated against all available data. Whilst the large confidence intervals predicted by the model suggest that large between-year variance in population size could be observed, the observed data exhibited much smaller between-year variance. Such confidence intervals implied larger than observed between-year variance, which could have resulted from my model structure, which allowed all parameters to vary independently. In reality, this assumption may not be met, for example if large clutch sizes result in lower per capita cygnet survival; however, there is currently a lack of data on such mechanisms within swan populations. Small observed variance around the mean predicted population change indicated that this mean is likely to most accurately reflect the change that would occur in response to population management. The large confidence intervals associated with the stochastic model are likely related to

the high within-parameter variance reported in field studies (Trump *et al*., 1994; Watola *et al*., 2003; **Chapter 5**). The finding that population-level outcomes were ergodic, *i.e.* not sensitive to initial population size or structure (Caswell, 2001), suggests that swan populations are controlled by processes such as survival and productivity rather than starting conditions. Other studies have also indicated ergodic population dynamics in swan populations (Perrins, 1991). The model made several assumptions that appear to be valid; the assumption of an equal sex ratio appears valid in light of the almost 1:1 ratio reported in **Chapter 5**. The model assumed a normal distribution around the mean for all parameters, which appears valid given (a) current understanding of swan population dynamics and (b) the accuracy of the model predictions compared with historical data (Perrins, 1991).

Whilst the three management techniques were predicted to reduce swan population sizes relative to no management, all were predicted to typically leave large swan populations within the catchment, even at high management intensities. For all but a sustained reduction in reproductive success to 0 eggs per nest, and the combined effects of very low reproductive success and high removals of individuals, the resulting stable population sizes were above the target of 155 individuals. Thus the strategies tested in this study are unlikely to alleviate the swan grazing conflicts alone or in combination except at very high management intensities. Furthermore, once management ceased at the end of the 50 year period, it is likely that population size would increase again, indicating that population management would have to continue indefinitely to remain successful. Population reductions may fail to occur because removed individuals (i) may represent compensatory rather than additive mortality, (ii) may be replaced by immigrant individuals, and (iii) productivity and survival may be negatively density-dependent (Fox, 2005). Comparisons of the predictions for each strategy in open and closed systems indicated that population reductions would be partially offset by immigration from outside of the catchment. Whilst the catchment may be a useful management unit for practitioners, highly mobile animals such as swans are able to move freely between different river catchments (Birkhead & Perrins, 1986; **Chapter 5**). Thus it may be more appropriate to consider swan population management at larger spatial scales. However, as ecologists we currently lack sufficient quantitative understanding of swan population dynamics at spatial scales larger than a single river catchment, which precludes expanding the current population model. High survival rates, particularly of the non-breeding adults which comprised the majority of the non-breeding subpopulation, probably also offset reductions due to population management; the sensitivity analyses showed that if survival rates were lower the predicted population size would be lower and thus smaller reductions would be required to decrease the population below the threshold. Thus the effectiveness of methods designed to reduce reproductive success or

remove non-breeding non-breeding individuals will likely be reduced in populations subject to high survival rates and high levels of immigration.

There are substantial practical and ethical obstacles to the successful implementation of the strategies tested in this study. Model predictions were based on 100 % efficiency of each management technique; in reality nests may not be detected and birds may escape capture or cull and thus no technique is likely to achieve 100 % efficiency. However, there are no data with which to evaluate the efficiency of large waterfowl population control techniques. An attempt to reduce the mute swan population of the Netherlands culled 25 % of the population *per annum* (Esselink & Beekman, 1991), which suggests that the high-levels of annual removal predicted to cause the greatest reductions in population size may be difficult to sustain over many years. Reductions in reproductive output in birds are most commonly achieved through clutch manipulation, which is most effective in species which nest at high densities or colonially as many nests can be manipulated for relatively little effort (*e.g.* Wright & Phillips, 1991). In chalk rivers mute swans nest at low densities and so greater effort would be required due to the greater area that would need to be searched (Trump *et al*., 1994; Watola *et al*., 2003; **Chapter 5**). For translocation, a lack of suitable sites at which to release swans may represent another obstacle; in Great Britain the mute swans population has undergone a substantial increase from 17,600 individuals in 1978 to 31, 700 in 2002, and is believed to have continued rising since (Kirby *et al*., 1994; Ward *et al*., 2007). Translocations also risk the transfer of the grazing conflict from one area to another (Kirby *et al*., 1999). Given this rapid and sustained increase it is doubtful whether translocation represents a sustainable management strategy. The levels of effort required for population control to successfully prevent the grazing conflict would likely be unacceptably high both to managers, due to the sustained high levels of time and effort required, and to the public, due to sustained high levels of interference with the swan population. Mute swans are protected under the EU Wild Birds Directive (2009/147/EEC), implemented in the UK through the Wildlife and Countryside Act (1981), making it illegal to capture, kill or injure swans, or to disturb or damage swan nests or eggs. Translocation, culling, clutch manipulation and fertility control all breach current UK law; such measures could be licensed where swans are demonstrated to cause substantial ecological or economic damage, but in practice more ethical methods of alleviating the conflict such as habitat management would first have to have been explored and demonstrated to be ineffective. Currently, there are few published data on the efficacy of different habitat management strategies and other ethical interventions on alleviating the conflict associated with swans in chalk rivers. Further research should test whether changes in habitat management could alleviate the conservation conflict associated with swans in chalk rivers due to overgrazing. Chalk river plant stands and associated biota could be protected by the establishment of sacrificial feeding areas near to areas of overgrazing, as have been suggested for other waterfowl grazing conflicts

(Owen, 1977; Vickery *et al*., 1994; Amano *et al*., 2007). Sacrificial feeding areas have been used to successfully alleviate a swan grazing conflict with agriculture in the River Tweed catchment in Scotland (Spray *et al*., 2002).

This study provides evidence that attempts to reduce population size are less effective when the target population is subject to (i) high levels of immigration and (ii) high individual survival rates. Large herbivorous waterfowl such as geese and swans frequently meet these two criteria, being highly mobile and relatively long-lived (Perrins, 1991). In accordance with the predictions of our model, field studies have reported that populations of swans and geese are able to withstand large annual removals of individuals; annual removal of up to 40 % of the total number of individuals does not cause total population size to decline (Imber & Williams, 1968; Vikberg & Moilanen, 1985; Schaeffer *et al*., 1987; Esselink & Beekman, 1991; Sladen, 1991). Given the limitations of population control, it is questionable whether such control should be attempted for populations subject to high levels of immigration and high survival, unless concurrent measures to reduce immigration and individual survival rates can also be employed. These results highlight the need to assess the effects of different combinations of management techniques on population sizes. Population models, such as the one presented here, can provide a cost-effective and ethical means to facilitate such assessments.

Chapter 7: Go with the flow: water velocity regulates swan foraging profitability in river catchments.

7.1 Abstract

Foragers typically attempt to consume food resources that offer the greatest energy gain for the least cost. Highly-mobile foragers such as waterfowl can switch between habitats as the most profitable food resource changes over time. Such switches are frequently observed in shallow river catchments, with negative consequences of foraging on the river ecosystem. However, the factors which cause these seasonal switches from terrestrial to aquatic habitats are unknown. I used an optimal foraging model to examine the effect of seasonal changes in food quantity, food quality and foraging costs on the timing of a switch from terrestrial to aquatic habitat by non-breeding mute swans (*Cygnus olor*). To accurately predict this switch date I needed to include seasonal variance in foraging costs in the model. However, I did not need to include seasonal variance in food quantity and food quality, as accurate predictions could be obtained with fixed values for these two parameters. Therefore, the seasonal changes in foraging costs were the key factor influencing the decision of the swans to switch feeding habitats. These seasonal changes in foraging costs were driven by changes in water velocity; the profitability of aquatic foraging was negatively related to water velocity, as faster water required more energy to be expended in swimming.

7.2 Introduction

Explaining the spatiotemporal patterns of animal diet and distribution that we see in nature is a central challenge facing ecologists. The most common explanation holds that foragers should attempt to select the habitat and diet that allow them to maximise their intake rate of energy and nutrients over time whilst minimising metabolic foraging costs and risk of exposure to harmful stimuli (*e.g.* toxins) and predation (Stephens & Krebs, 1986; Newman *et al*., 1995; Killen *et al*., 2007). The most profitable food resource is that which yields the greatest energy gain for the lowest cost. Three key factors can determine what the most profitable diet should be, and consequently where the animals should feed; food quantity, food quality and foraging costs (Stephens & Krebs, 1986). Increases in both the quantity and nutritional quality will increase the profitability of a food resource, making it more attractive to foragers (Owen, 1972; Owen-Smith & Novellie, 1982; Illius *et al*., 1999). In contrast, increased foraging costs lower the profitability of a

food resource. Foraging costs may be direct costs such as the energy expenditure required to capture and consume a prey item, or indirect costs such as increased predation risk (Stephens & Krebs, 1986). The quantity, quality and costs associated with a given food resource can vary in space and time, causing animals to move within and between habitats in order to obtain the most profitable food resources (Prins & Ydenberg, 1985; Vickery *et al*., 1995). These predictions of optimal diet theory have been upheld in a range of different field tests (*e.g.* Goss-Custard, 1970; Owen-Smith & Novellie, 1982; Nolet *et al*., 2001; Babin *et al*., 2011). The theory has proven particularly robust for animals which feed on immobile prey, such as herbivores consuming plant tissues (Sih & Christensen, 2001). In particular, highly mobile taxa such as herbivorous waterfowl (Order: Anseriformes) can obtain different diets by switching between different habitats; switches are frequently documented between aquatic habitats where they feed on submerged macrophytes, and agricultural land where they feed on crops or fertiliser-enriched grasses (Nolet *et al*., 2001; **Chapter 5**).

Shallow river catchments contain key habitats for waterfowl, which move seasonally between feeding in the river itself to adjacent terrestrial pastures (Trump *et al*., 1994; Mason & Macdonald, 2000; **Chapter 5**). Shallow river plant communities, which may be regulated by waterfowl herbivory (O'Hare *et al*. 2007; **Chapter 4**), support high levels of secondary production, in particular of invertebrates and fish (Berrie, 1992) . Such plants are also integral to the hydrological and biogeochemical functioning of shallow river ecosystems (Clarke, 2002; Cotton *et al*., 2006). Understanding the factors which regulate the timing and duration of waterfowl use of shallow rivers could allow the manipulation of such factors to facilitate ecosystem management, for example to reduce waterfowl grazing. Thus, understanding what determines when and why waterfowl switch from terrestrial to aquatic feeding is critical to understanding the structure and functioning of shallow river ecosystems. However, I am not aware of any studies to date which have examined waterfowl foraging profitability in any flowing-water ecosystem.

In this study I used an optimal foraging model to examine whether seasonal changes in food quantity, food quality or foraging cost, or a combination of these three factors, explained the observed shift from terrestrial to aquatic habitat (**Chapter 5**). Such models have been used previously to successfully predict herbivore diet (Owen-Smith & Novellie, 1982; Newman *et al*., 1995; Inger *et al*., 2006). Changes in the relative profitability of aquatic and terrestrial food resources are believed to cause a diet (and thus habitat) shift in non-breeding mute swans (*Cygnus olor* Gmelin, 1789) (**Chapter 5**; **Chapter 8**). These swans exhibit a seasonal switch between foraging in the river on submerged aquatic plants in summer and autumn, and foraging in terrestrial pasture fields on pasture

grasses in winter and spring (**Chapter 5**). Swans enter the river between April and May, and may cause localised grazing damage thereafter (O'Hare *et al*., 2007; **Chapter 4**). In shallow rivers foraging costs are likely to be regulated by water velocity, which determines the energy required for movement. Thus at higher water velocities a forager must expend more energy swimming (Prange & Schmidt-Nielsen, 1970). Indeed, the period when non-breeding swans use the river coincides with the lowest seasonal water velocity values (Bowes *et al*., 2005). Thus, I tested four alternative hypotheses; swan foraging profitability would be determined by seasonal changes in (*H1*) food quantity, (*H2*) food quality, (*H3*) foraging costs, or (*H4*) a combination of two or more of these factors.

7.3 Methods

7.3.1 Study system

This study was undertaken in the catchment of a mesotrophic chalk river, the River Frome (Dorset, UK), from Maiden Newton (50°46'N, 02°34'W) 44 km downstream to West Holme (50°41'N, 02°10'W). The main river channel is dominated by the aquatic plant stream water crowfoot (*Ranunculus penicillatus ssp. pseudofluitans* (Syne) S.D. Webster) (O'Hare *et al.,* 2007). The river is typically bordered by terrestrial pasture fields dominated by perennial ryegrass (*Lolium perenne* L.), creeping bentgrass (*Agrostis stolonifera* L.), and Yorkshire fog (*Holcus lanatus* L.), which frequently become water-logged during winter.

7.3.2 Plant collections

I selected 20 river sites on the main channel of the River Frome that were characteristic of the river in terms of morphology, hydrology and plant community; these were the same sites detailed in **Chapter 4**. Pasture grass was repeatedly sampled from the pasture field adjacent to each of the river sites; however, at two sites there was no pasture field and thus I sampled from 20 river sites and 18 pasture fields. Quantitative samples of water crowfoot (n = 10 cores per month) and pasture grass (n = 5 cores per month; **Appendix 5**) were taken monthly from March to September 2010 using a 0.00785 m^2 hand corer following the methodology of described in **Chapter 4**. Cores were taken from each field from randomly-generated coordinates. For pasture grass, sward height (± 0.5 cm) was measured at the centre of each core. All samples were bagged, labelled and taken to the laboratory, where non-plant material and excess water were removed, before fresh mass (± 0.01 g) was measured on a Sartorius PT120 balance (Sartorius GmbH, Germany). The plant sample was then dried to constant mass at 60 °C in a Heraeus Kelvitron T oven

(Thermo Fisher Scientific, Loughborough, UK), reweighed and the dry matter (DM) biomass (± 0.01 g) was recorded.

7.3.3 Food quantity

Each month the quantity of each food plant, water crowfoot and pasture grass, were estimated as the mean of all samples taken in that month. I estimated food quantity as dry matter biomass (g DM m^{-2}). A pasture grass functional response (*sensu* Holling, 1959) of Bewick's swans (*Cygnus columbianus bewickii* Yarrell, 1830), a congener of the mute swan, has been reported by van Gils *et al*. (2007). Bewick's swan intake rate (I_{Bew}, in g DM s^{-1}) was reported as:

$$I_{Bew} = (a \cdot (1.38 \cdot 10^{-3} \cdot H)) / (a \cdot b + (1.38 \cdot 10^{-3} \cdot H)) / 60$$

where H was the sward height in cm, and a and b were the bite size and handling time (3.6 and 0.02 respectively) derived by van Gils *et al*. (2007). I modified this equation so that intake rate was expressed for a given pasture grass biomass (B, in g DM m^{-2}) rather than sward height (H, in cm); using the sward height and biomass data from my 18 field sites, I found a significant, positive relationship between mean sward height and biomass for all months at all sites (Linear regression: $F_{1,124} = 211.9$, $p < 0.0001$, $R^2_{adj} = 63$ %; **Figure 7.1**). Thus I converted sward height to sward biomass according to the following relationship:

$$H = 0.0238 \cdot B$$

My results in Chapter 2 demonstrated that pasture grass intake rates scale with waterfowl body mass according to the following equation:

$$Log_{10} = -4.89 + 0.81 \cdot LogM$$

where M = body mass (g). I used this equation to calculate the relative difference between the intake rates of Bewick's (0.0148 g DM s^{-1}) and mute (0.0238 g DM s^{-1}) swans, assuming body mass values of 6000 g and 10800 g respectively (Kear, 2005). I calculated the intake rate of a mute swan relative to a Bewick's swan as:

$$0.0238 \text{ g DM } s^{-1} / 0.0148 \text{ g DM } s^{-1} = 1.61$$

Thus I estimated the intake rate for mute swans feeding on a given food biomass as:

$$I_{Mute} = I_{Bew} \cdot 1.61$$

where I_{Mute} and I_{Bew} were the intake rates (g DM s^{-1}) of mute and Bewick's swans respectively.

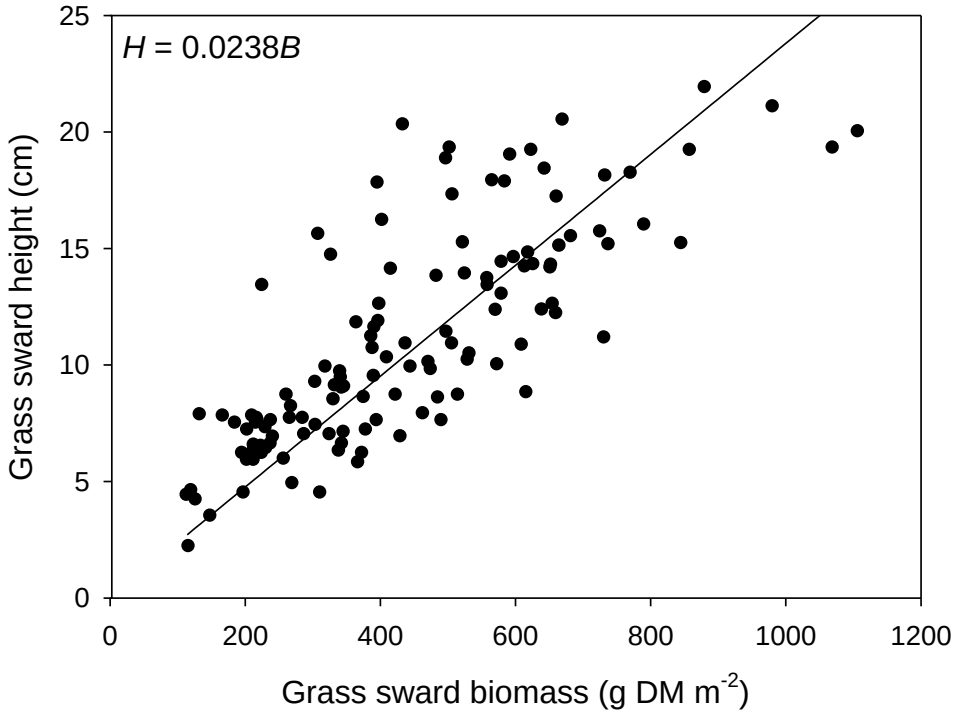


Figure 7.1: *The relationship between the mean height and biomass of pasture grass swards.*

As the functional response for above-ground aquatic plants had not been quantified for any swan species, I conducted feeding trials of mute swans on water crowfoot in November 2009 at Abbotsbury Swannery, Dorset, UK (50°39'N, 02°36'W). Five randomly-selected adult swans, two males and three females, were placed in individual pens (average area = 33.6 m^2) consisting of a pond surrounded by a sand embankment. Ages ranged from 3 to 8 years (median 6). For the first six days, each bird was presented with water crowfoot *ad libitum* in 0.15 m^2 black plastic trays, 435 mm (l) x 335 mm (w) x 90 mm (d), in order to acclimatize them to the feeding trial conditions. Fresh water crowfoot was obtained daily from the River Frome at East Stoke (50°41'N, 02°11'W), and strands were drawn at random for use in the trials; only healthy strands with leaves present were selected. On the seventh day feeding trials commenced; each bird was presented once per day with a predetermined biomass of water crowfoot in its tray and allowed to feed for 180 ±10 s. Trays were filled with clear water and placed at the shallow edge of the pond. The water crowfoot strands were arranged to cover the largest possible surface area inside the tray in order to maintain a constant foraging area. Each feeding trial was filmed using a tripod-mounted Canon Legria HFS10 HD video camera (Canon Inc., Japan) and all observers left the feeding area to minimise disturbance. After excess

water was removed with paper towel, macrophyte biomass was weighed before (R_b) and after (R_a) each trial using a Pesola PTS3000 balance (Pesola AG, Switzerland). Any water crowfoot that had been removed from the tray but not consumed was counted as 'wastage' (R_w) and weighed separately. Consumption was calculated as:

Consumption = R_b - (R_a + R_w)

Twelve water crowfoot fresh biomasses, reflecting biomasses reported in field studies, were presented to each bird during the trials; 50 g m^{-2}, 75 g m^{-2}, 100 g m^{-2}, 150 g m^{-2}, 200 g m^{-2}, 300 g m^{-2}, 500 g m^{-2}, 750 g m^{-2}, 1000 g m^{-2}, 1500 g m^{-2}, 2000 g m^{-2}, and 3000 g m^{-2} (O'Hare *et al.*, 2007; **Chapter 3**; **Chapter 4**). Both the order in which each bird received the different macrophyte biomasses, and the order in which each bird was tested each day, were randomised. All individuals had access to grit and water *ad libitum*. As these feeding trials were not considered a procedure, as defined in the Animals (Scientific Procedures) Act 1986, I did not require a Home Office licence.

7.3.4 Food quality

I measured the nutritional quality of water crowfoot and pasture grass, in terms of energy content, at four of our sites between March and September. Randomly selected samples (n = 3) from four river and four adjacent field sites were ground for 300 s at 25 Hz in a Retsch MM200 Ball Mill (Retsch GmbH, Germany). This sub-sampling approach was used as it was not economically-viable to analyse samples from all sites; these four sites were selected as they were characteristic of the catchment in terms of land use, sediment composition and plant community. Prior to analyses samples were redried at 105 °C for three hours in a Gallenkamp Prime Oven (Weiss Gallenkamp, Loughborough, UK). To determine energy (kJ g^{-1}) content 0.20 ± 0.01 g DM of each sample was analysed using a 1109 semi-micro oxygen bomb and 6200 Oxygen Bomb Calorimeter (Parr Instrument Company, USA). To calculate the metabolisable energy content I multiplied the plant energy content values by swan digestibility values for pasture grass (0.327; van Gils *et al*., 2008) and aquatic macrophytes (0.523; O'Hare *et al*., 2007).

7.3.5 Foraging costs

Mute swan BMR (kJ s^{-1}) was calculated as:

BMR = ($VO_2 \cdot m$) $\cdot$ e

where VO_2 was the consumption of oxygen (ml O_2 g^{-1} s^{-1}) as reported in Bech (1980), *m* was mean swan mass (10800 g) as given in Kear (2005), and *e* was the energy yielded per ml of oxygen consumed (kJ ml^{-1} O_2) assuming a conversion of 0.02 kJ ml^{-1} O_2 (Nolet *et al.,* 2002). Thus I estimated mute swan BMR as 0.039 kJ s^{-1}. I calculated the energetic cost of terrestrial foraging as the multiple of basal metabolic rate (BMR) reported for a congenital species, the Bewick's swan, in Nolet *et al*. (2002), yielding a mean ± 95 % CI value of 0.047 ± 0.022 kJ s^{-1}. Whilst BMR increases with mean body mass across species, the metabolic costs of behaviours as a multiple of BMR are consistent between closely related, morphologically-similar species such as mute and Bewick's swans (Bruinzeel *et al*., 1997). To estimate the energetic cost of aquatic foraging, I calculated the cost of swimming at a given water velocity (*L*; m s^{-1}) using the relationship between the multiple of BMR ($_x$BMR) and swimming speed for northern mallard (*Anas platyrhynchos* L.) reported by Prange & Schmidt-Nielsen (1970) as such data for swans were not available (**Figure 7.2a**):

$$_x\text{BMR} = 4.0 + -12.2L + 15.4(L^{\wedge 2})$$

Based on my derived mute swan BMR (0.039 kJ s^{-1}) I calculated the metabolic cost (*FC*; in kJ s^{-1}) of swimming at a given water velocity as:

$$FC = {}_x\text{BMR}_L \cdot \text{BMR},$$

where $_x\text{BMR}_L$ was the multiple of BMR for a given value of *L* (kJ s^{-1}). Thus I estimated the relationship between the metabolic cost (*FC*; in kJ s^{-1}) of swimming at a given water velocity (**Figure 7.2b**) as:

$$FC = 0.16 + -0.48L + 0.60(L^{\wedge 2})$$

As mute swans and northern mallards are closely related (Order: Anseriformes) they have a highly similar morphology and swimming action. Furthermore, as functionally similar surface-swimming birds both species have the same hull design, a displacement hull, and it is this hull design which determines the shape of the relationship between energy expenditure and water velocity (Prange & Schmidt-Nielsen, 1970). Therefore I expected an equivalent BMR-swimming speed relationship for both species. Daily mean water discharge (m^3 s^{-1}) measurements between 1st March and 31st September 2010 were provided by the Environment Agency for the East Stoke gauging station (station number 44001; 50°41'N, 02°11'W), from which daily mean water velocity (m s^{-1}) values were calculated for this period (**Figure 7.3**). Because water discharge, velocity, and channel cross sectional area (width multiplied by depth) are interrelated according to the relationship, discharge = velocity · cross sectional area, I carried out a back calculation of

velocity that was based on the standard technique used to derive depth–discharge relationships for gauging station rating curves, although in this instance velocity, not depth was derived (Bovee & Milhouse, 1978; Gordon, 1992). River cross sections were available for East Stoke, recorded using the methods described in **Chapter 3**. Only four cross sectional areas were available and hence some caution was necessary in interpreting the results, however it is known that three points are sufficient to extrapolate within the range 40 – 250 % of calibrated flow (Bovee & Milhouse, 1978). Mean cross sectional velocity (L, in m s^{-1}) was calculated according to the formula:

$$L = a \cdot (1 - \exp(-b \cdot Q)),$$

where Q was the mean discharge (m^3 s^{-1}), whilst a (1.44; **Chapter 3**) and b (0.12; **Chapter 3**) were the intercept and slope of the relationship between channel morphology and discharge.

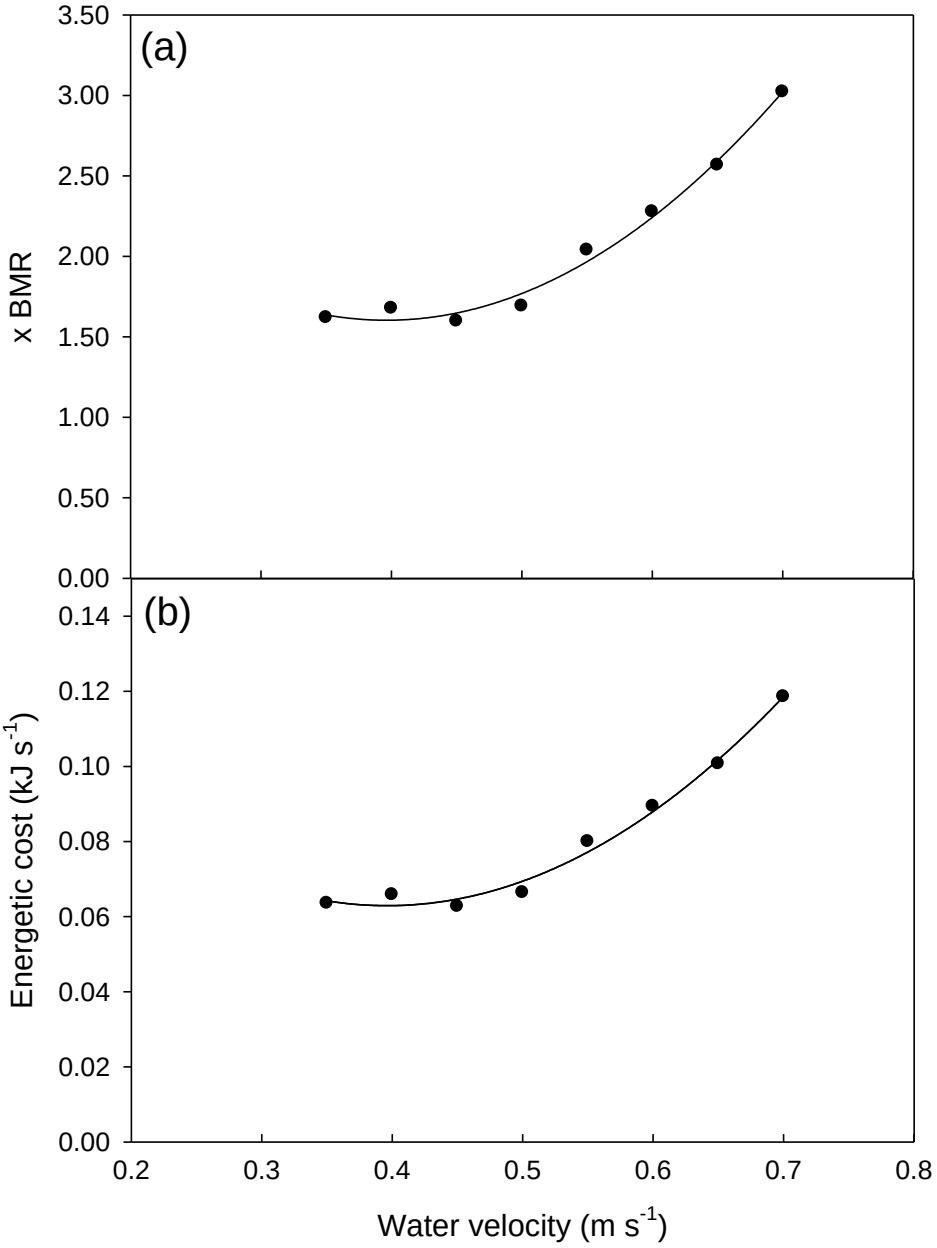


Figure 7.2: *The cost of swimming at a given water velocity, expressed as (a) the multiple of BMR and (b) the metabolic cost in kJ* s^{-1}.

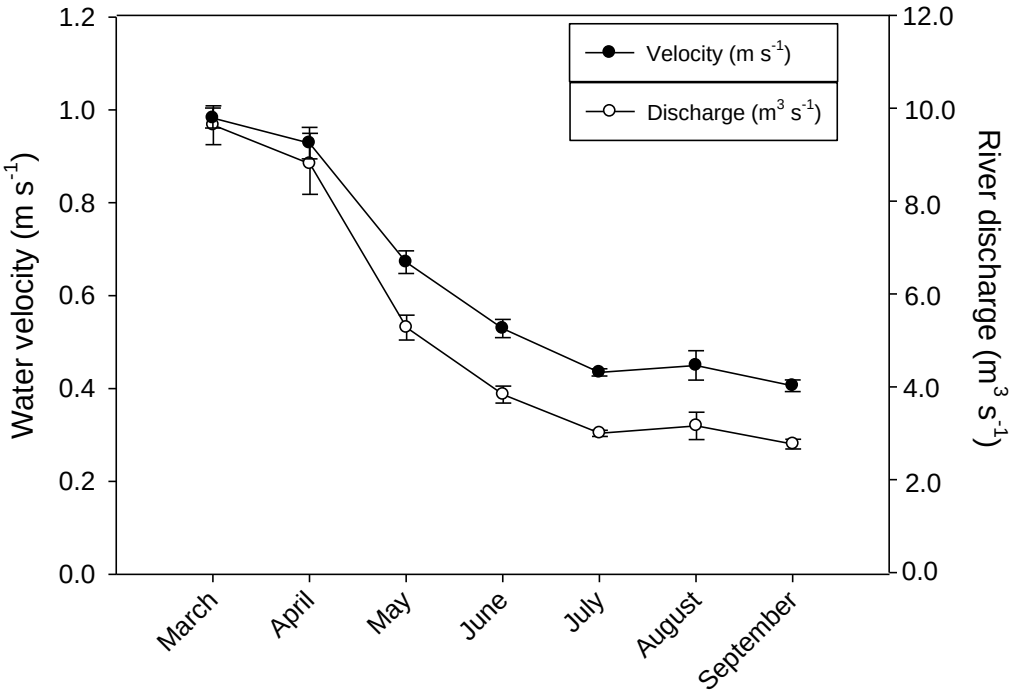


Figure 7.3: *Monthly changes in mean ± 95 % CI gauged discharge and calculated velocity for the study area.*

7.3.6 Foraging models

I used a model to calculate the profitability of a swan foraging in aquatic and terrestrial habitats each month between March and September. I compared these profitability values to predict when swans should switch between habitats, assuming that swans should always feed on the most profitable food resource. In each model the profitability (rate of energy gain, in kJ s^{-1}) of the two food resources was determined by the equation:

Profitability = $((FQI \cdot d) \cdot I_{FQn}) - FC$,

where *FQI* was the gross energy content (kJ g^{-1} DM), d was the digestibility as a proportion of the gross energy content, I_{FQn} was the intake rate (g DM s^{-1}) for a given biomass value of *FQn* (g DM m^{-2}), and *FC* was the metabolic cost of foraging (kJ s^{-1}).

I sequentially tested all eight combinations of models of fixed and variable values for food quantity (FQn; g DM m^{-2}), food quality (FQI; kJ g^{-1} DM) and foraging costs (FC; kJ s^{-1}). Where parameters were variable, the mean value for each month was used. Where parameters were fixed, the mean value for the March to September was used. This

approach allowed me to examine how the profitability of the two food resources changed under conditions of fixed or variable food quantity, food quality and foraging costs, and assess how such changes affected the food resource swans were predicted to exploit. The 'best' model was the one which required the fewest parameters to predict a habitat switch between April and May (**Chapter 5**; **Figure 5.5**), as this model was the most parsimonious in terms of data required.

7.4 Results

7.4.1 Food quantity

When foraging on water crowfoot swan intake rate (I, in g DM s^{-1}) increased with food density (B, in g DM m^{-2}) according to the relationship $I = (0.0031\ (\pm\ 0.0006) \cdot B) / (1 + (0.0934\ (\pm\ 0.0207) \cdot B))$ (**Figure 7.4**). Over the same range of food densities for pasture grass there was also a positive relationship between food density and intake rate, although intake rate was lower than for water crowfoot (**Figure 7.4**). Water crowfoot biomass exhibited a strong seasonal pattern, increasing from 38.5 g DM m^{-2} in March to a seasonal maximum of 576.4 g DM m^{-2} in July, declining thereafter (**Figure 7.5a**). Pasture grass biomass showed a gradual but uneven increase across the study period, rising from 333.8 g DM m^{-2} in March to 566.9 g DM m^{-2} in September (**Figure 7.5a**). Mean biomass values for the March to September period were 297.8 g DM m^{-2} and 439.7 g DM m^{-2} for water crowfoot and pasture grass respectively.

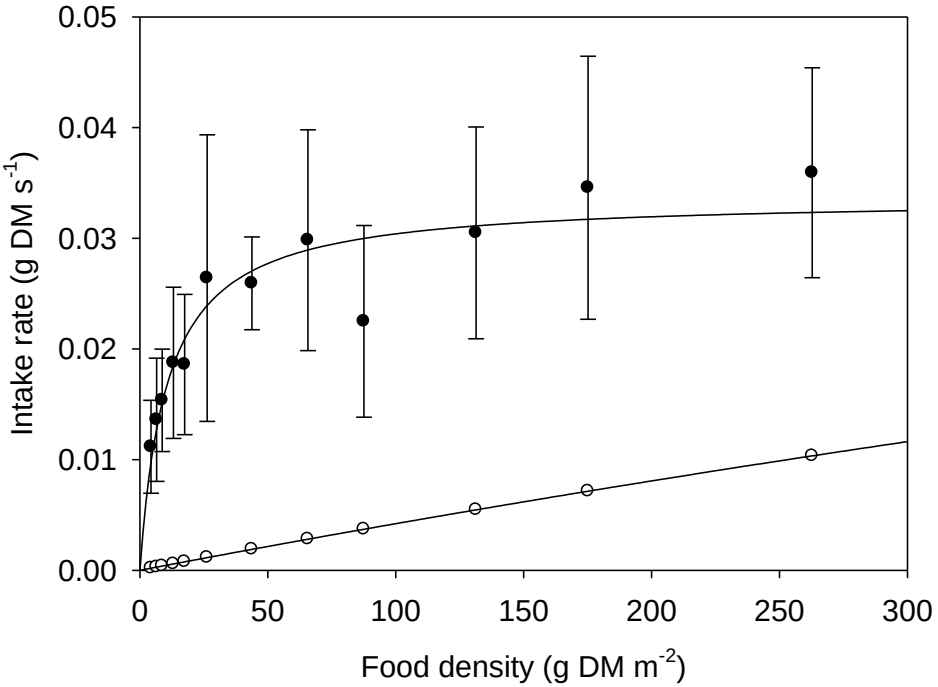


Figure 7.4: *The mean (± 95 % CI) mute swan intake rates when feeding on water crowfoot (solid markers) and pasture grass (open markers).*

7.4.2 Food quality

Limited between-month variance was found in the mean (± 95 % CI) gross energy content of water crowfoot (13.4 ± 0.2 kJ g^{-1} DM) and pasture grass (15.8 ± 0.3 kJ g^{-1} DM) (**Figure 7.5b**). No consistent seasonal trend in energy content was observed for either plant.

7.4.3 Foraging costs

In all months the cost of aquatic foraging was higher than the cost of terrestrial foraging. Whilst the cost of terrestrial foraging did not vary (0.047 kJ s^{-1}), the cost of aquatic foraging declined over the study period from 0.270 kJ s^{-1} in March to 0.063 kJ s^{-1} in September (**Figure 7.5c**). This decline in aquatic foraging costs was driven by the seasonal decline in mean (± 95 % CI) water velocity from 0.98 (± 0.02) m s^{-1} in March to 0.41 (± 0.01) m s^{-1} in September (**Figure 7.3**). The mean foraging cost for the March to September period was 0.125 kJ s^{-1}.

7.4.4 Foraging models

All four models in which foraging costs were a variable parameter correctly predicted that the habitat switch should occur between April and May (**Figure 7.6**). In contrast, none of the four models in which foraging costs were a fixed value indicated that the relative profitability of aquatic and terrestrial foraging should change. The accuracy of the model predictions was not influenced by whether food quantity or food quality were fixed or variable parameters (**Figure 7.6**).

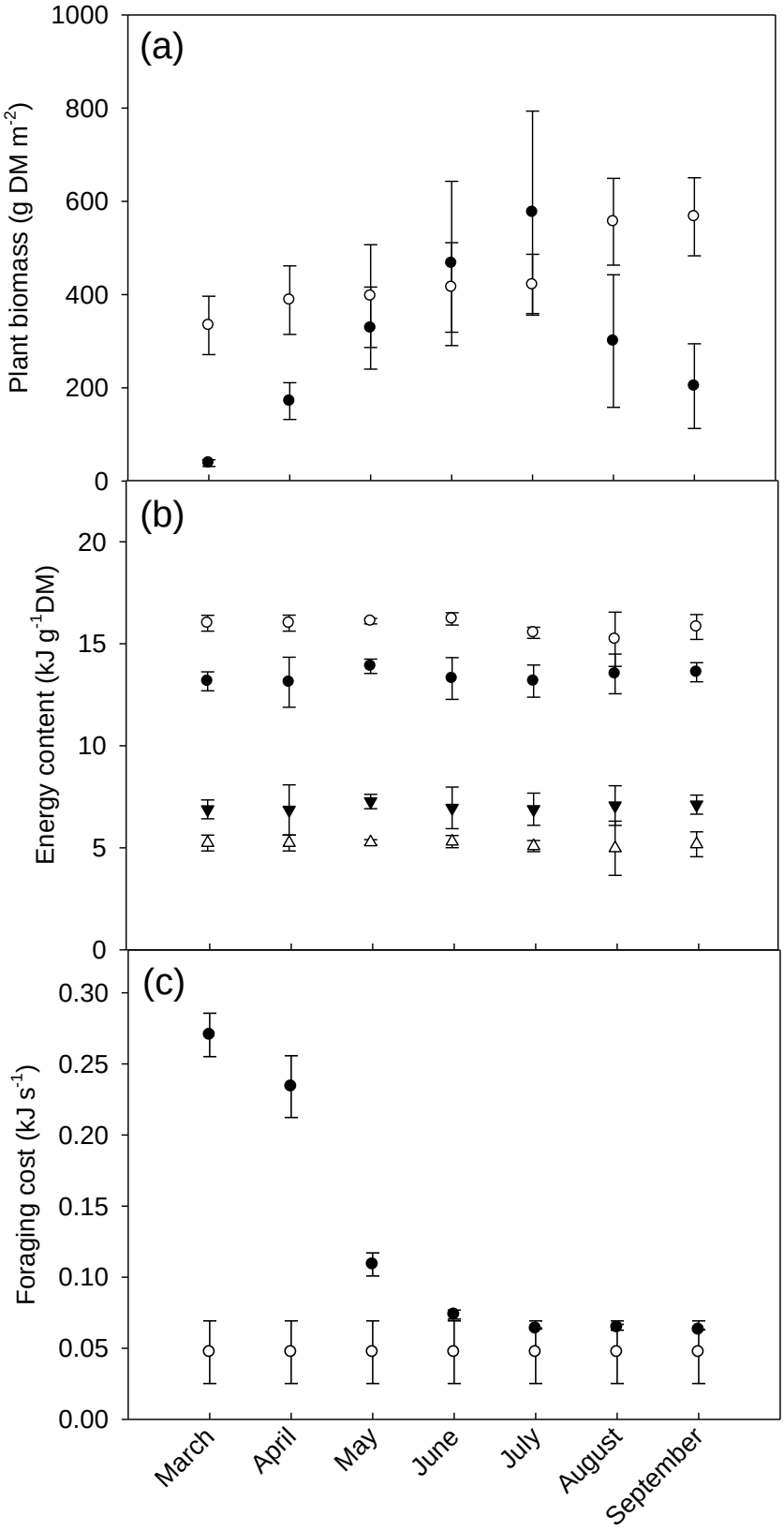


Figure 7.5: *Monthly changes for water crowfoot (solid markers) and pasture grass (open markers) in terms of mean ± 95 % CI (a) dry weight biomass, (b) gross (circles) and metabolisable (triangles) energy content, and (c) foraging costs.*

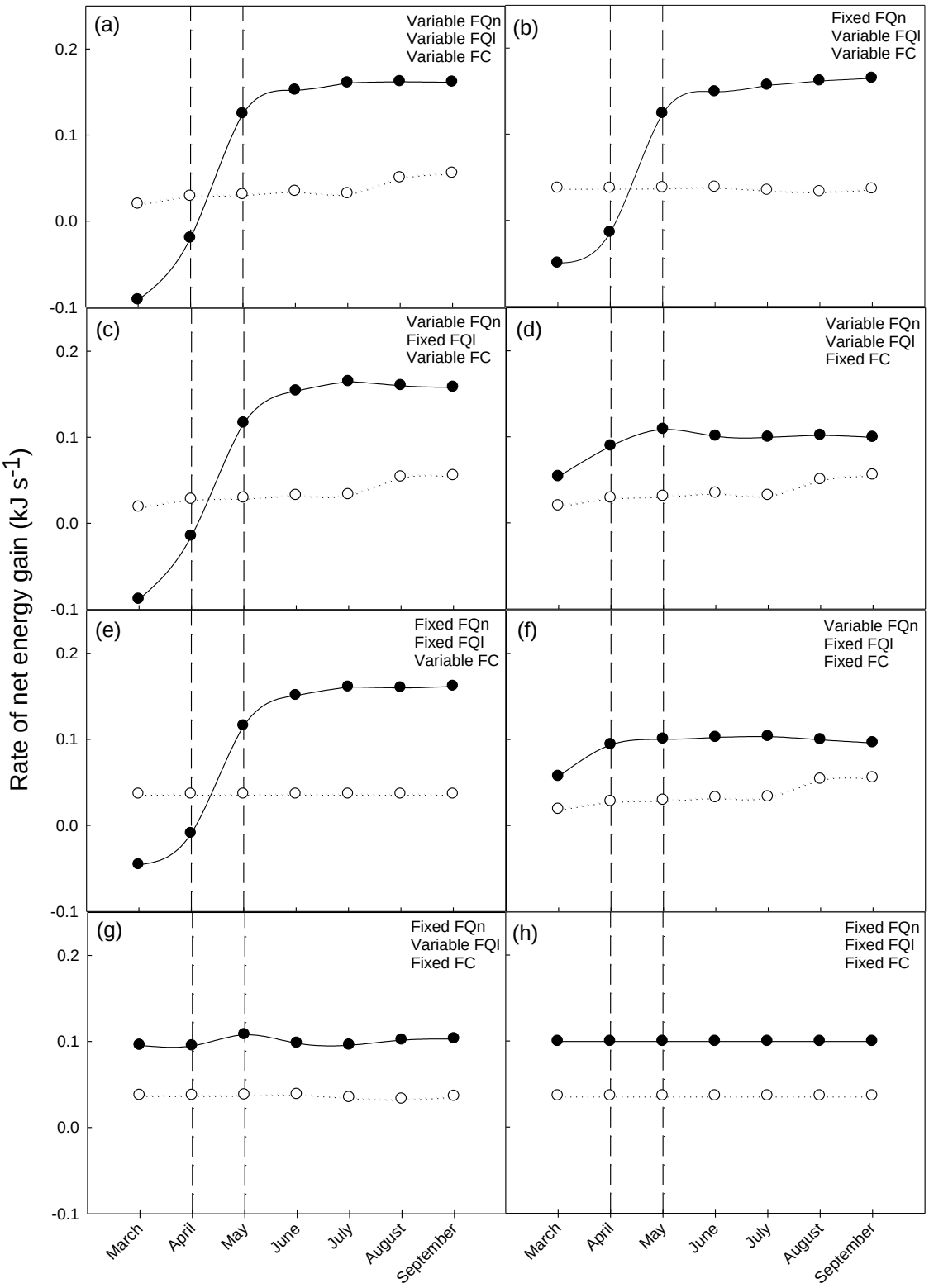


Figure 7.6: *The changes in swan foraging profitability (rate of net energy gain in kJ s^{-1}) for water crowfoot (solid circles) and pasture grass (open circles) predicted by our foraging models (a-h). The observed diet and habitat switch occurred between April and May, indicated by the dashed lines.*

7.5 Discussion

In this study I have, for the first time, examined how a switch in herbivore foraging habitats is regulated by the water velocity of the aquatic habitat. Previous studies of switches between terrestrial and aquatic habitats have not addressed flowing waters. Previous studies have examined the effect of varying water depth on the availability (*i.e.* food quantity) of rooted submerged plants to waterfowl (Mather *et al*., 1998; Clausen, 2000; Nolet *et al*., 2006), but this is the first study to examine how changes in water velocity influence foraging and habitat choice. This study offers a mechanistic understanding, based on the gains and costs associated with different food resources, of forager shifts between alternative habitats.

To accurately predict the date when swans would switch from terrestrial to aquatic foraging, I needed to include seasonal variance in foraging costs in our model. However, I did not need to include seasonal variance in food quantity and food quality, as accurate predictions could be obtained with fixed values for these two parameters. Therefore, although my study was correlational, the results suggest that the seasonal changes in foraging costs may have been a key factor influencing the decision of the swans to switch feeding habitats, supporting my third hypothesis (*H3*). These seasonal changes in foraging costs were driven by changes in water velocity; the profitability of aquatic foraging was negatively related to water velocity, as faster water required more energy to be expended swimming (Prange & Schmidt-Nielsen, 1970). For this same reason, the costs of non-foraging activities would also higher in the river compared with the terrestrial habitat. Therefore swans might delay switching to the river until the net rate of energy gain whilst foraging compensates for the additional metabolic cost of non-foraging activities in flowing waters. Further study of the pasture to river switch at a higher temporal resolution (*e.g.* daily rather than monthly) could examine how the relative daily energy expenditures for both habitats vary over this period.

Food quantity in the river increased more steeply than in pasture fields between March and July and therefore could have potentially explained the observed habitat shift; however, the models suggested that these changes in food quantity alone did not affect the relative profitability of the two food resources. The models assumed no seasonal changes in the digestibility associated with each food resource; whilst gut length (positively related to digestibility) can undergo seasonal changes in response to long-distance breeding migrations in migratory swan species (*e.g.* van Gils *et al*., 2008), there is no such evidence for sedentary species such as mute swans (Bruinzeel *et al*., 1997).

Bech (1980) demonstrated that mute swans are thermoneutral between 1 and 15 °C, and so metabolic rate does not vary with temperature within this range; given that water temperatures in chalk rivers such as the River Frome seldom vary outside of this range (Berrie, 1992), and air temperatures were only likely to have exceeded 15 °C around midday in the summer period (June-August), the influence of temperature on metabolic rate was unlikely to have affected the model predictions around the habitat switch between April and May. Foraging costs were not assumed to vary for terrestrial habitats, as there are no known changes in the terrestrial pasture environment that would alter foraging costs over the study period. In contrast, the drop in aquatic foraging costs between April and May changed the relative profitability of aquatic and terrestrial foraging in favour of aquatic plants. Before April, foraging costs were so high that swans would lose energy even whilst foraging. This may explain why paired birds, which in contrast to flocks remain at the river over winter to defend their territory, have been observed to spend much of their time on the bank or in the slack water in the river margins, rather than in the main channel (Scott, 1984; Birkhead & Perrins, 1986). My work suggests that such behavioural strategies are necessary to maintain a territory throughout winter whilst avoiding a negative energy balance (Scott, 1984). Lower water velocities in the early part of the study period would likely cause an earlier habitat switch and thus a longer period of grazing on river plants. I did not have the data to examine the reverse shift from river to pasture that has been observed between October and November (**Chapter 5**). However, water velocity is known to increase in response to the seasonal increase in precipitation which occurs during this period, which suggests that changes in water velocity may again drive this swan habitat shift later in the year (Bowes *et al*., 2005).

My results suggest that the length of the swan grazing season in shallow rivers is likely to be related to water velocity, as lower velocities allow swans to enter the river sooner due to reduced costs of foraging. Previous research has shown that the growth of shallow river plant communities is inhibited by low water velocities (Westlake, 1967). My study indicates that such plants will also be negatively impacted by lower water velocities due to a longer swan grazing season. Therefore, measures to increase water velocity, for example by modifying channel morphology, could benefit shallow river plants by increasing growth and delaying the onset of grazing. However, changes in food quantity within the low foraging cost habitat, caused by depletion, may cause shifts between different river reaches if velocity is relatively constant or between different pasture fields (*i.e.* movements within-habitat types) (O'Hare *et al*., 2007; **Chapter 8**). This contrasts with some other study systems where between-habitat differences in foraging costs are small and thus depletion of food resources can drive switches between habitat types (*e.g.* Vickery *et al*., 1995; Rowcliffe *et al*., 2001).

In shallow rivers the seasonal decrease in water velocity from March to September, linked to a decrease in precipitation, is also associated with a decrease in turbidity (Dawson, 1981). However, I would argue that this increase in water clarity cannot explain the swan habitat shift onto the river; swans are thought to be tactile feeders, using their highly-sensitive bill to locate submerged food (Kear, 1988). Such tactile, rather than visual, food location may explain why swans are frequently observed to feed in highly-turbid water bodies, and to consume plant storage organs (*e.g.* tubers) buried within sediments (Nolet *et al*., 2001; Gayet *et al*., 2011). There are several other factors known to influence profitability and thus habitat switching. Forager distribution can be influenced by human disturbance, with animals typically moving to areas of low disturbance (Gill *et al*., 1996; Holm *et al*., 2011). However, given that the River Frome catchment is largely private agricultural land with little public access and low levels of disturbance, I consider that human activities were unlikely to have affected swan distributions in this study. Where predation risk differs between habitats this may also influence distribution, with foragers selecting feeding habitats by making a trade-off between maximising energy gain and minimising predation risk (Holbrook & Schmitt, 1988; Fortin *et al*., 2005; Searle *et al*., 2008). However, few animals in Britain can kill a swan and thus predation risk is minimal, accounting for just 3 % of annual adult mortality (Brown *et al*., 1992). Additionally, there is no evidence to suggest that predation risk for swans differs between river and pasture habitat, thus predation was unlikely to have been an important factor affecting distribution. Therefore I can be confident that the change in the relative profitability of swan food resource and associated habitat switch is driven by changes in water velocity rather than by confounding or correlated factors.

As the values of water crowfoot energy content (13.4 kJ g^{-1} DM) are the first to be reported, I cannot assess potential variation between different river catchments. However, it is slightly lower than the 16.6 kJ g^{-1} DM and 16.4 kJ g^{-1} DM reported by Boyd (1970) for broadleaf water milfoil (*Myriophyllum heterophyllum* Michaux, 1803) and hornwort (*Ceratophyllum demersum* L.) respectively, two functionally and morphologically similar aquatic plants. The mean pasture grass energy content of 15.8 kJ g^{-1} DM was close to the 17.6 kJ g^{-1} DM reported by van Gils *et al*. (2008) for a similar lowland pasture field in the Netherlands. The relative lack of change in the quality of pasture grass through the spring growth period could be explained by the presence of grazing cattle (*Bos primigenius* L.), which may have maintained the swards at a relatively constant quantity and quality. Whilst pasture grass had a higher gross energy content, the lower digestibility and intake rate meant that pasture grass offered a lower rate of metabolisable energy gain compared with water crowfoot.

This study indicates the importance of comparing values of relative profitability for different available food resources within a landscape. Crucially, such comparisons must include estimates of the energetic costs of foraging on each food resource, not just the gross gains. Highly mobile foragers such as waterfowl can track the most profitable food resource as seasonal changes in foraging costs occur.

Chapter 8: Can we manipulate the profitability of swan food resources to protect aquatic plants from herbivory?

8.1 Abstract

Foraging mute swans can cause substantial depletion of aquatic plant abundance in chalk rivers in southern England and this can adversely affect ecological and economic interests. A key requirement for a catchment management strategy is to understand where grazing pressure will be greatest, and how changes to management can reduce grazing pressure. To assess the suitability of using ecological models for this purpose, I constructed and tested an individual-based model (IBM) of swans foraging on a section of the River Frome and adjacent pasture in Dorset, England. IBMs, which predict the behaviour and movement of individual animals within a population on the basis that foragers attempt to maximise their perceived fitness, have previously been used to test management strategies to resolve a range of wildlife conflicts. The model predicted the swan carrying capacity, plant biomass depletion, swan feeding time, and feeding patch use. I used this model to test the effects of two management options on the depletion of aquatic plants by swans; (i) the addition of a sacrificial crop, and (ii) increasing water velocity through altered river management. The net rate of energy gain available to pasture-feeding swans was too low to make improved grass an effective sacrificial crop. The water velocity required to force the swans from river to pasture was high, requiring a mean increase of 58 %. However, only marginal increases in water velocity were required to achieve a shift between a modified and unmodified river reach, and so could be used to prevent the grazing conflict on a local scale. This study highlights the potential use of IBMs as tools to evaluate options designed to help reconcile management conflicts in river catchments.

8.2 Introduction

Plants are fundamental to the structure, function and service provision of many ecosystems (Grime, 2002). Herbivores can have a range of effects on plants, typically reducing abundance and altering morphology, growth rates, productivity, species richness and evenness (Cyr & Pace, 1993; Milchunas & Lauenroth, 1993; Côté *et al.*, 2004; **Chapter 2**; **Chapter 4**). Where such effects impact negatively on ecological or economic aims, management may be required to alleviate such impacts. Management may be costly, in terms of both time and money; additionally, there may also be ethical issues where herbivores are charismatic *i.e.* popular with the public (Ellis & Elphick, 2007). To avoid wasted effort and needless controversy it is necessary to evaluate the

probability of any proposed management strategy achieving a defined objective. We can conduct such evaluations using individual-based models (IBMs), which predict the behaviour and movement of individual animals within a population from simple behavioural rules, principally that foragers attempt to maximise their perceived fitness (Grimm & Railsback, 2005; Stillman & Goss-Custard, 2010; **Figure 8.1**). As such, IBMs are useful tools with which to explore interactions between consumers and their resources, and how such interactions may be affected by changes in the environment. IBMs have previously been used to test management strategies to resolve a wide range of wildlife conflicts, such as those between geese and agricultural crops, large felids and human livestock, and between shorebirds and shellfisheries (Ahearn *et al*., 2001; Stillman *et al*., 2001; Stillman *et al*., 2003; Amano *et al*., 2004).

The chalk rivers of southern and eastern England are of high conservation value. Chalk rivers support high abundances of invertebrates and fishes, in particular salmonid species such as brown trout (*Salmo trutta* L.) and Atlantic salmon (*S. salar* L.) (Berrie, 1992). These salmonid populations, coupled with the high aesthetic quality of chalk river, support economically valuable game fisheries (Ladle & Westlake, 1976). The ecological and economic value of chalk rivers is due in part to the high abundances of the submerged macrophyte water crowfoot (*Ranunculus spp*.), which increases physical wetted volume of the river and provides habitat, shelter and food for other organisms (Hearne & Armitage, 1993; Armitage & Cannan, 2000). Reduced production of submerged macrophytes may result in lower invertebrate production and diversity, as well as reduced salmonid population densities and individual body size (Riley *et al*., 2009). In recognition of the keystone role of water crowfoot it is protected under the EU Habitats and Species Directive (92/43/EEC). However, grazing by flocks of mute swans (*Cygnus olor* Gmelin, 1789) can reduce both macrophyte abundance and flowering, as well as alter community structure in chalk rivers (O'Hare *et al*., 2007; **Chapter 4**). In pasture fields adjacent to the rivers, swans can also decrease grass abundance and thus increase feed costs for livestock farmers (Harrison, 1985). A grazing conflict thus exists, whereby flocks of swans may reduce the high conservation status and economic value of chalk river catchments (Fox, 1994; Trump *et al*., 1994; Parrott & McKay, 2001b).

In view of the potential for ecological economic damage, there is a need to manage the swan grazing conflict in chalk rivers. To date there have been several unsuccessful attempts to find an appropriate management strategy. Two separate modelling studies have predicted that swan population control, even at intensive levels, would still leave large flocks present as reductions are offset by local breeding and immigration from outside the catchment (Watola *et al*., 2003; **Chapter 6**). Parrott & McKay (2001b) used

nesting platforms to encourage pairs to nest and thus defend the surrounding reaches, but the platforms were not used and grazing by flocks occurred. In some cases electric fences have been used to successfully exclude swans from short reaches (*e.g.* Fox, 1994). However, electric fencing is undesirable due to the hazard it poses to river users, such as anglers and people in canoes.

Highly-mobile herbivores such as swans can move between different feeding locations and food resources in order to maximise their net rate of energy gain, *i.e.* metabolic gain minus costs; Perry & Pianka, 1997; Sih & Christensen, 2001; **Chapter 7**). Understanding these drivers of herbivore movements enables the possibility of manipulating such drivers in order to reduce or prevent grazing on ecologically or economically valuable plant communities. The provision of sacrificial feeding areas to which birds can move has been suggested as a cost-effective management option to alleviate waterfowl grazing conflicts (Owen, 1977; Vickery *et al*., 1994; Amano *et al*., 2007). The provision of a sacrificial feeding area successfully alleviated a grazing conflict between mute swans and crops of oilseed rape (*Brassica napus* L.) in the River Tweed catchment, Scotland (Spray *et al*., 2002). Alternatively, increasing the water velocity in river reaches, for example through narrowing the river channel or adjusting water management, could increase the metabolic cost of river feeding to swans and so trigger a shift to either terrestrial habitat or river reaches with lower velocity (**Chapter 7**).

In this study I developed and tested an IBM for a population of swans in a chalk river, and used this model to test the effects of two management options on reducing the the depletion of aquatic plants by swans; (i) the addition of an additional field of a sacrificial crop, and (ii) increases in water velocity.

8.3 Methods

8.3.1 Study area

The River Frome (Dorset, UK) is a mesotrophic chalk river that flows through a catchment dominated by pastoral agriculture. The pasture grass community is dominated by three species; perennial ryegrass (*Lolium perenne* L.), creeping bentgrass (*Agrostis stolonifera* L.) and Yorkshire fog (*Holcus lanatus* L.) (**Chapter 5**), which are all consumed by swans (Rees, 1990). The aquatic plant community is dominated by stream water crowfoot (*Ranunculus penicillatus ssp. pseudofluitans* (Syne) S.D. Webster) (**Chapter 3**; **Chapter 4**), which is also consumed by swans (O'Hare *et al*., 2007). The river is shallow and is

typically less than 1 m deep (Dawson & Robinson, 1984; **Chapter 3**). The catchment has a mean population of 298 swans; the flock subpopulation switches between feeding in terrestrial pasture field in winter and spring to feeding in the river in summer and autumn (**Chapter 5**).

8.3.2 Grazing model

MORPH is a flexible IBM which makes few species- or system-specific assumptions and has thus been used extensively to evaluate the responses of foraging animals to changes in their environment (Stillman, 2008; **Figure 8.1**). MORPH has been described extensively by Stillman (2008). In this study MORPH was parameterised and tested for a 1.1 km length of the River Frome and an adjacent pasture field at East Stoke (Dorset, England; 50°41'N, 02°11'W) for 22 days in May, during the swan grazing season (O'Hare *et al*., 2007; **Chapter 4**; **Chapter 5**). In the model the 1.1 km length of river was considered a single patch, hereafter referred to as the river patch. A value was assigned to each parameter required by the model (Stillman, 2008) from either field or literature data (**Table 8.1**) for this river patch (9153 m^2) and one adjacent field patch (95000 m^2). Initial water crowfoot biomass, growth rate over the study period, and the biomass of water crowfoot outside of the study area, were those given by O'Hare *et al*. (2007). Grass biomass in the pasture field was estimated as the mean of the mean May and June 2010 values, as determined from the 18 sites reported in **Chapter 7**. At each site in May and June 2010, 5 cores were taken from each field using a 0.00785 m^2 hand corer; all above-ground biomass was removed, dried to constant weight at 60 ˚C using a Heraeus Kelvitron T oven (Thermo Fisher Scientific, Loughborough, UK), and weighed to ± 0.01 g on a Sartorius PT120 balance (Sartorius GmbH, Germany). Mean grass biomass was set to 406.0 g DM m^{-2}, and grass biomass change over time (in the absence of swan grazing) was set to 0.0 g m^{-2} d^{-1}, as a T-test indicated no significant difference between grass biomass in May (mean 396.7 g DM m^{-2} ± 251.6 s.d.) and June (mean 415.3 DM g m^{-2} ± 219.1 s.d) (T = -0.24, d.f. = 34, p = 0.814), probably due to grazing by cattle (*Bos primigenius* L.). Gross energy content for pasture grass and water crowfoot were those given in **Chapter 7** for the River Frome in May, whilst proportional digestibility values were those given by van Gils *et al*. (2008) and O'Hare *et al*. (2007).

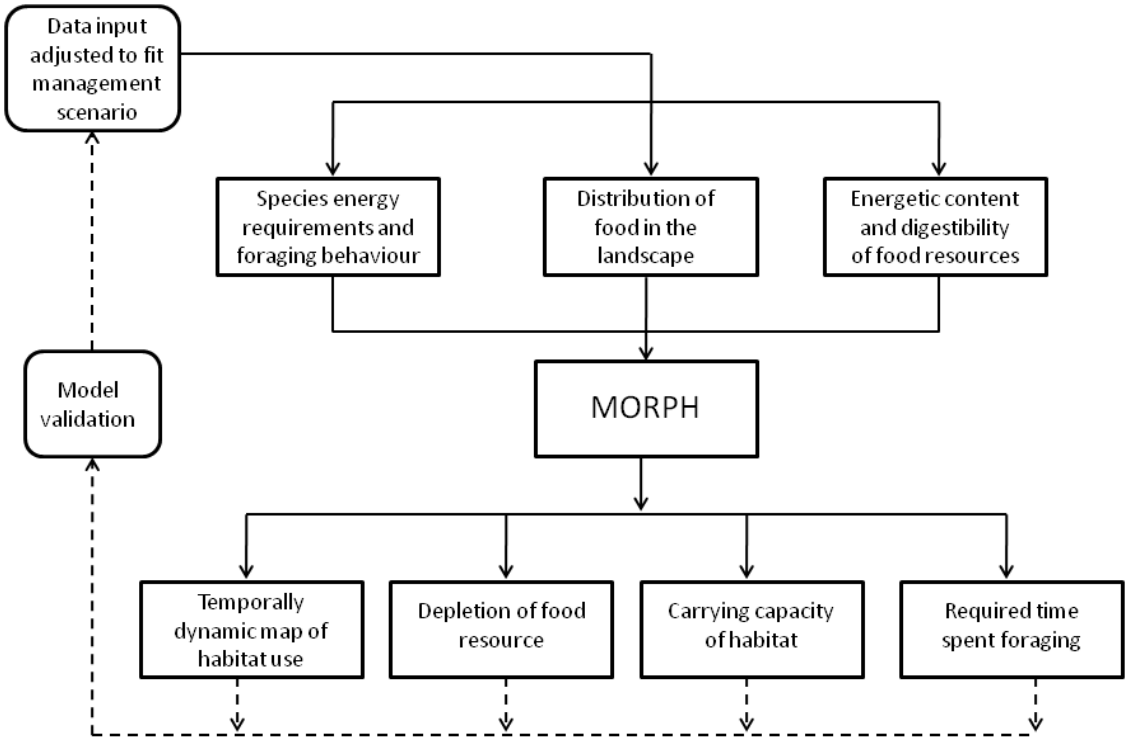


Figure 8.1: *A concept diagram of the individual-based modelling process using 'MORPH', illustrating the key parameters required (inputs) and the predictions generated (outputs).*

The model ran in hourly time-steps. Based on the times of dawn and dusk at our site I distinguished between daylight (06:00-20:00), when foraging was permitted, and darkness (21:00-05:00), when birds were not permitted to forage as field evidence suggests mute swans do not feed at night (Jozkowicz & Gorska-Klek, 1996; Meissner & Ciopcińska, 2007). Swans exploited their food resources according to the functional responses given for water crowfoot and pasture grass given in **Chapter 7**. Swans within the model could choose to rest or forage on either water crowfoot or pasture grass; metabolic costs of resting and foraging on each food resource were those given in **Chapter 7**. Swans in the model were assumed to maximise their net rate of energy gain

whilst foraging to maintain their internal energy store at a value of 150920 kJ. This energy store value was estimated as the energy content of avian tissue (34.3 kJ g^{-1}; Kersten & Piersma, 1987) multiplied by the difference between the mean mass and mass at starvation (10800 – 6400 g; Delany, 2005). Swans were assumed to have starved if this energy store was depleted to 0; a starvation event was recorded by the model and the forager concerned was removed from the model. If a swan could obtain a higher net energy gain in the river area outside of the model it would emigrate; thus swans could consider the profitability of the model patches against the profitability of the wider environment. All individuals were designated as non-breeding adults based on the information presented by O'Hare *et al*. (2007) and, as the study area was small, were permitted to move between patches between time steps. Initial exploration of the model indicated that, as the model used mean parameters only, results were consistent between model runs.

The predictions of the model were compared with three field observations given by O'Hare *et al.* (2007); (i) the carrying capacity of the study area (*i.e.* both patches combined) expressed as the number of swans multiplied by the number of days each swan was present within the study area, referred to as swan days; (ii) the water crowfoot biomass in the river patch at the end of the simulation, which was a measure of depletion by swan grazing; (iii) the percentage of swan days within both patches that were spent in the river patch, which was a measure of the relative use of river habitat. Additionally, I compared the prediction of the percentage of total time each day which swans spend feeding with field data collected in a time-budget study in the River Frome at East Stoke in May 2009 (**Appendix 6**).

***Table 8.1**: The values associated with each parameter in the model.*

Parameter	Value	Derivation
Initial number of swans	41	O'Hare *et al*. (2007)
Swan metabolic cost of river feeding	0.109 kJ s^{-1}	**Chapter 7**
Swan metabolic cost of pasture feeding	0.047 kJ s^{-1}	**Chapter 7**
Swan metabolic cost of resting	0.039 kJ s^{-1}	**Chapter 7**
Swan energy store	150920 kJ	This study
Initial water crowfoot biomass in study area	184.5 g DM m^{-2}	O'Hare *et al.* (2007)
Initial water crowfoot biomass outside study area	171.1 g DM m^{-2}	O'Hare *et al.* (2007)
Water crowfoot growth rate	0.0 g m^{-2} d^{-1}	Growth rate under swan grazing pressure as swans remove growth tissues (O'Hare *et al*., 2007)
Water crowfoot gross energy content	13.4 kJ g^{-1} DM	**Chapter 7**
Water crowfoot digestibility	0.523	O'Hare *et al.* (2007)
Swan intake rate I when feeding on water crowfoot biomass B	$I = (0.0031B) / (1 + (0.0934B))$	**Chapter 7**
Initial grass biomass	406.0 g DM m^{-2}	This study
Grass growth rate	0.0 g m^{-2} d^{-1}	This study
Grass gross energy content	15.8 kJ g^{-1} DM	**Chapter 7**
Grass digestibility	0.327	van Gils *et al.* (2008)
Swan intake rate I when feeding on pasture grass biomass B	$I = ((a \cdot (1.38 \cdot 10^{-3} \cdot (0.0238 \cdot B))) / (a \cdot b + (1.38 \cdot 10^{-3} \cdot (0.0238 \cdot B))) / 60) \cdot 1.6$	**Chapter 7**

8.3.3 Sensitivity analysis

I assessed the sensitivity of the model predictions to changes in the mean value of each parameter by a local sensitivity analysis using the one-at-a-time method (Hamby, 1994). Each parameter was sequentially subjected to (a) an increase of 25 % and (b) a decrease of 25 %. Fixed percentage changes were used instead of estimates of error as these were unavailable for many parameters.

8.3.4 Management options

To test the effect of the provision of a sacrificial pasture field on the depletion of aquatic plant biomass by swans, I added an additional patch (17000 m^2) of fertiliser-enriched pasture grass of a biomass of 203.8 g DM m^{-2}, hereafter termed 'improved pasture grass'. By using the same biomass and functional response for both the standard pasture grass and improved pasture grass patches allowed me to separate the effects of increased quality from any confounding effects of changing the quality, of the food resource. I considered the effects of (i) increased gross energy content, (ii) increased digestibility, and (iii) combined increases in gross energy content and digestibility, of improved pasture grass. To address increased gross energy content I ran 31 model scenarios, varying the gross energy content between 10.0 and 40.0 kJ g^{-1} DM in 1.0 kJ g^{-1} DM increments. To address increased digestibility I ran 36 model scenarios, varying the proportional digestibility between 0.25 and 0.60 in 0.01 increments, reflecting the range of plant digestibility values reported for swans (Durant, 2003). Finally, to address combined increases in gross energy content and digestibility I ran all 1116 possible combinations of the 31 gross energy content values and 36 digestibility values in the previous simulations.

To test the effects of increases in mean water velocity on the depletion of water crowfoot biomass by swans I evaluated two scenarios; the flow speed required to shift swans from river to pasture, and the flow speed required to shift swans from one river reach to a river reach with a different flow speed. To evaluate the option of a pasture-river shift, I ran 71 model scenarios, varying water velocity between 0.50 and 1.20 m s^{-1} in 0.01 m s^{-1} increments, reflecting the range of water velocity values reported for chalk rivers (Armitage & Cannan, 2000). I used the relationship between the metabolic cost of swimming (z; in kJ s^{-1}) and water velocity (L; in m s^{-1}) given in **Chapter 7**:

$$Z = 0.16 + -0.48L + 0.60(L^{\wedge 2})$$

I then compared the change in mean May velocity to the actual velocities observed in May 2009 and 2010; I calculated mean monthly velocity for the period January 2009 to December 2010 from discharge values provided by the Environment Agency for the East Stoke gauging station, using the method presented in **Chapter 7**.

To evaluate the option of a river-river shift, I varied the flow speed and hence cost of river feeding inside the model patch whilst maintaining the flow speed of river feeding outside the model at a constant of 0.674 m s^{-1}, corresponding to a metabolic cost of 109 kJ s^{-1}; flow speed inside the model was varied between 0.50 and 1.20 m s^{-1} in 0.01 m s^{-1} increments, corresponding to a range of metabolic costs of 0.070 and 0.448 kJ s^{-1}; thus 71 model scenarios were run.

8.4 Results

8.4.1 Grazing model

The model predicted a carrying capacity for the study area (*i.e.* all patches) of 214 swan days, close to the 215 observed in the field. The predicted mean water crowfoot biomass after grazing (*i.e.* depletion) of 169.1 g m^{-2} closely matched the 171.1 g m^{-2} observed. The mean percentage of time spent by swans on river patches was predicted to be 100 %, slightly higher than the 98 % observed. Additionally, predicted daily time spent foraging (38 %) was within the range in a time budget study in May in the River Frome (mean ± 95 % CI = 32 % ± 12 %; **Appendix 6**). The percentage of swans which were predicted to starve during the model runs was 0 % (*i.e.* no mortality), which matched the field observations of O'Hare *et al*. (2007).

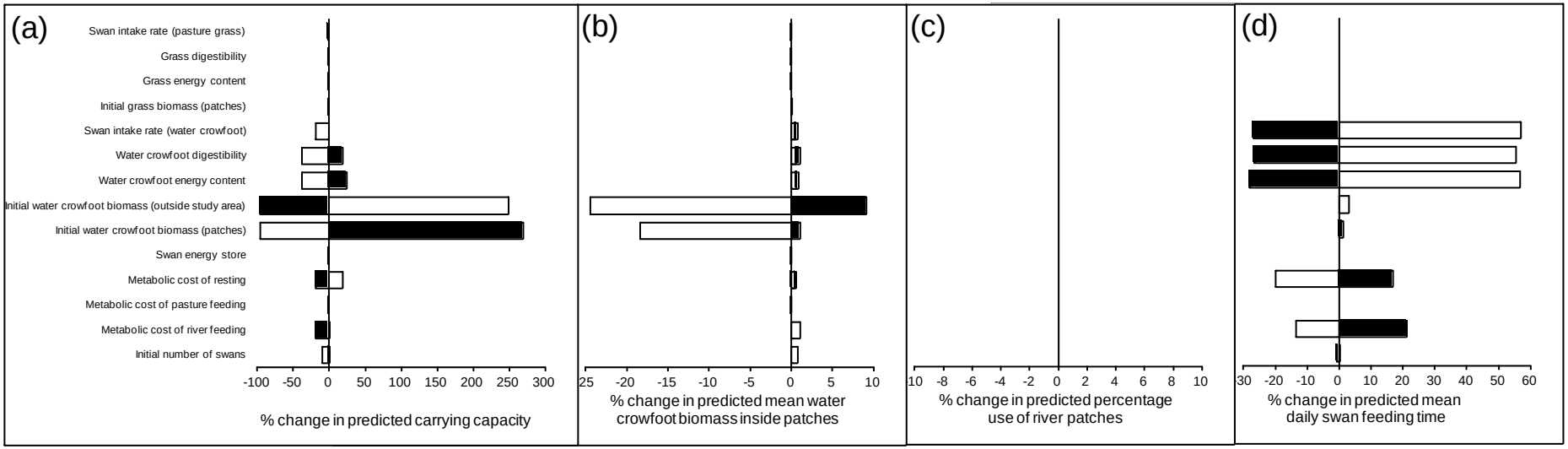


Figure 8.2: *The changes to predicted (a) carrying capacity, (b) aquatic plant biomass, (c) percentage use of the river patch, and (iv) swan daily feeding times in response to a 25 % increase (solid bars) or decrease (open bars) in the value assigned to each parameter.*

8.4.2 Sensitivity analysis

The model predictions of carrying capacity were most sensitive to changes in the initial water crowfoot biomass within the model patches as well as outside the study area (**Figure 8.2a**). Similarly, predictions of water crowfoot biomass after grazing were also affected most strongly by changes in the initial water crowfoot biomass in the patches and outside of the study area (**Figure 8.2b**). In contrast, the predictions of the relative use of the two patch types (river and pasture) were insensitive to changes in all parameters (**Figure 8.2c**). Predictions of swan daily feeding times were most sensitive to changes in parameters which regulated the rate of energy gain, in particular the intake rate, gross energy content, digestibility, and feeding costs associated with water crowfoot (**Figure 8.2d**).

8.4.3 Management options

The model predicted that swans would switch to feeding on improved pasture grass, thus preventing depletion of water crowfoot, at an improved pasture grass gross energy content of 36.0 kJ g^{-1} DM or greater (**Figure 8.3a**), or at an improved pasture grass digestibility of 0.58 or greater (**Figure 8.3b**). Where values for either gross energy content or digestibility were increased, this meant that a lower value was required for the other parameter in order to achieve a switch away from river feeding; for example, an increase in digestibility from 0.33 to 0.50 led to a reduction in the gross energy content required to cause the river-pasture shift from 35 kJ g^{-1} DM to 23 kJ g^{-1} DM (**Figure 8.3c**). Where swans switched, improved pasture grass biomass was predicted to be depleted from 406.0 to 377.0 g DM m^{-2}.

A water velocity of 0.87 m s^{-1} or greater was predicted to cause a shift from river to pasture feeding, thus preventing the depletion of water crowfoot (**Figure 8.4a**). An increase in mean May velocity to 0.87 m s^{-1} would represent a 70 % increase on May 2009 and a 45 % increase on May 2010 (**Figure 8.5**). Where swans switched, pasture grass biomass in the standard pasture grass field was predicted to be depleted from 406.0 to 399.3 g DM m^{-2}. Swans were predicted to emigrate out of the model area on the first time step if water velocity was higher in the model patch relative to outside the model; for the flow speed of 0.67 m s^{-1} outside the model, immediate emigration occurred whenever within-model flow speed was above this value (**Figure 8.4b**).

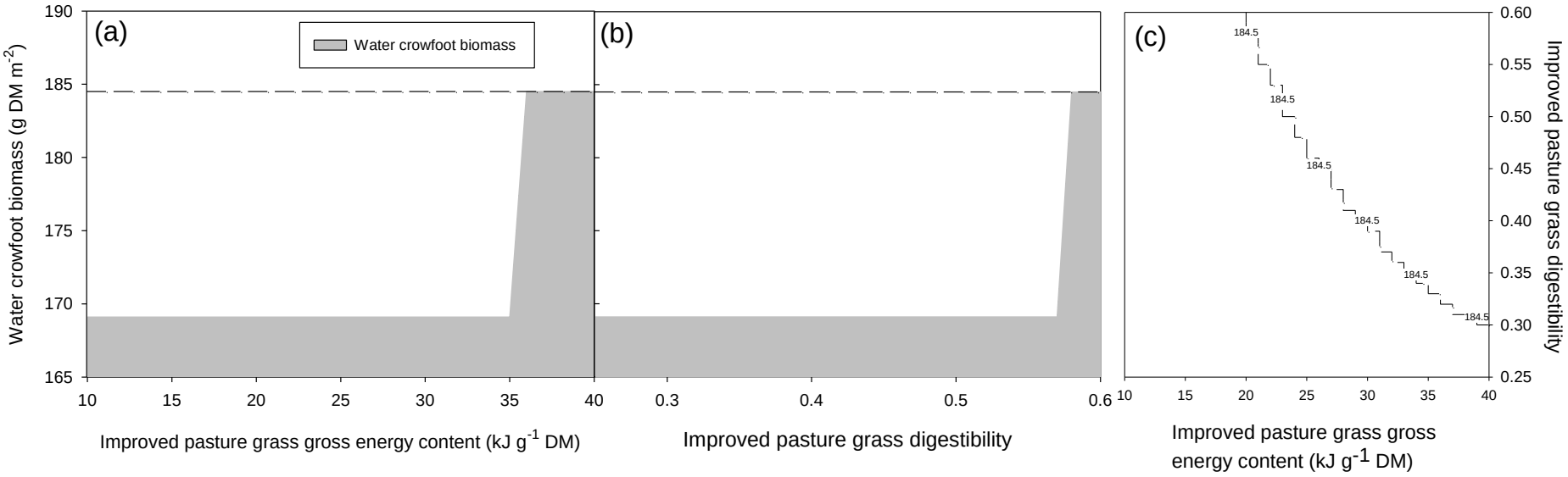


Figure 8.3: *The biomasses of water crowfoot at the end of the study period relative to (a) the gross energy content and (b) digestibility, and (c) the combined effects of gross energy content and digestibility on the threshold at which grazing depletion of water crowfoot will cease. The dashed line represents the starting biomass of 184.5 g DM m^{-2}; values below and left of this threshold in (c) indicate depletion by grazing.*

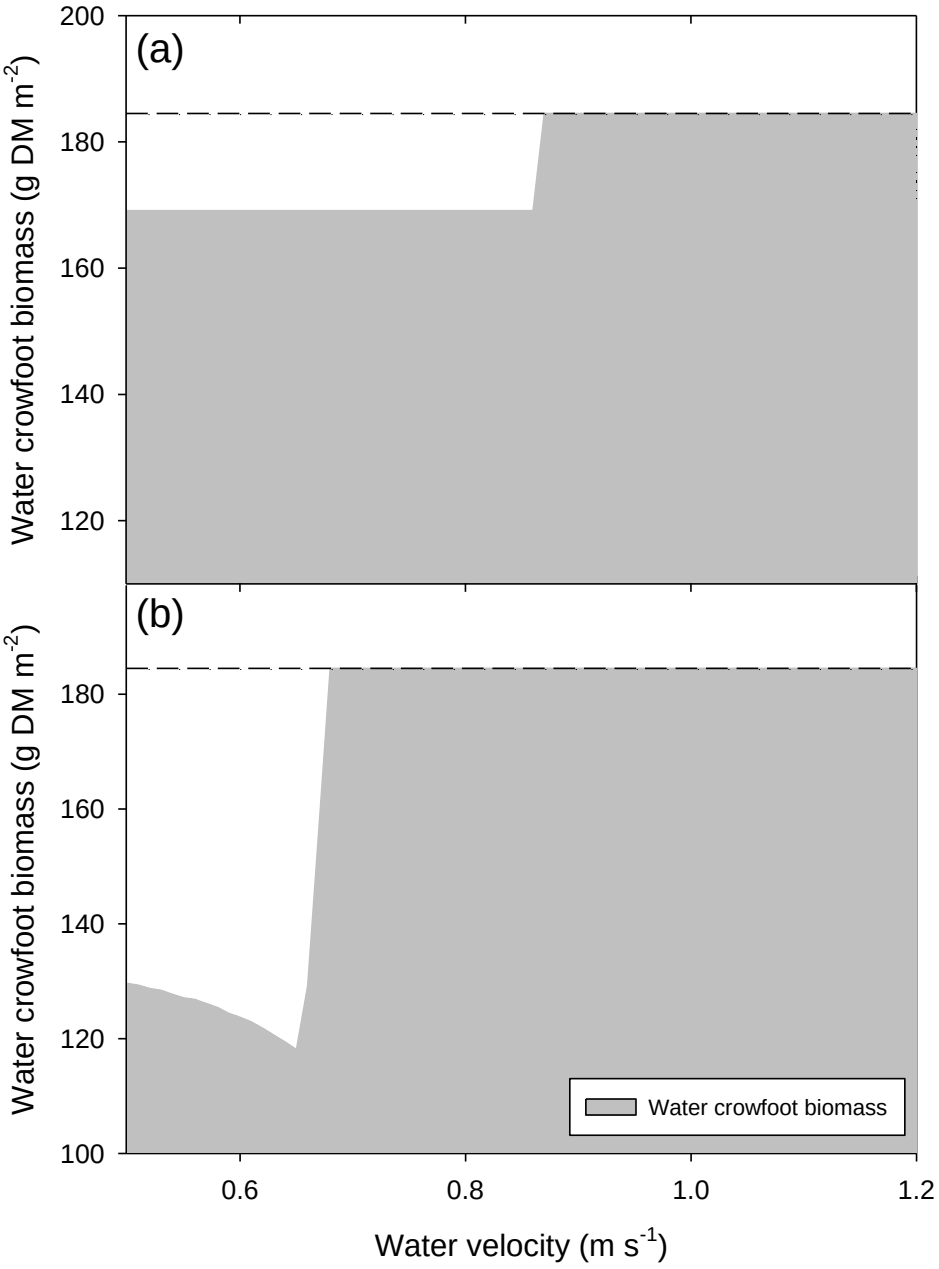


Figure 8.4: *The biomass of water crowfoot at the end of the study period relative to water velocity, which regulates the cost of feeding on water crowfoot, based on two management scenarios; (a) an attempt to achieve a river-pasture shift by an increase in water velocity within the model patch; (b) an attempt to achieve a river-river shift by an increase in water velocity inside the model patch, with no change outside the model area. The dashed line represents the starting biomass of 184.5 g DM* m^{-2}*; values below this threshold indicate depletion by grazing.*

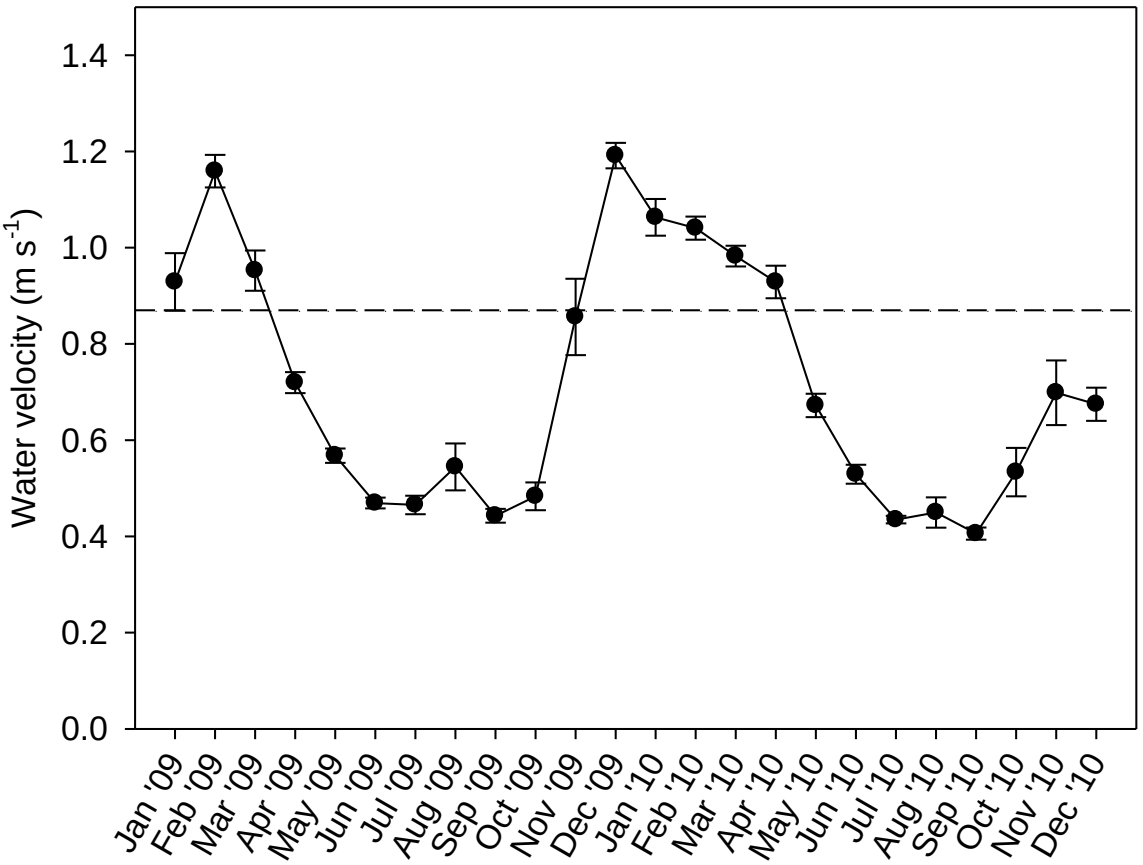


Figure 8.5: *Mean (± 95 % CI) water velocity values for the River Frome over a two year period. The dashed line indicates the threshold of 0.87 m* s^{-1}*, above which the model predicted swans should switch from river to pasture feeding.*

8.5 Discussion

The approach used in this study demonstrated how an understanding of the rules which determine foraging behaviour can be used to evaluate management solutions to wildlife conflicts. The knowledge that swans move to the location which offers the highest rate of energy gain (Sih & Christensen, 2001; **Chapter 7**) enabled me to use an IBM to predict the effects of two management options which manipulated the relative profitability of the available food resources. The model predicted that both the sacrificial field of improved pasture grass and increased water velocity could, above threshold levels, cause the swans to switch away from the river within the model and thus prevent the depletion of water crowfoot. Therefore, this study offers two possible options for habitat modifications to alleviate the grazing conflict in chalk rivers.

Combining increases in improved pasture grass gross energy content with simultaneous increases in digestibility facilitated a switch from river to improved pasture at lower values of gross energy content and digestibility (and thus management effort) than increases in either parameter in isolation. Digestibility of grasses could be improved by (i) managing the sward to achieve a high leaf:stem ratio of biomass allocation as leaves typically have higher digestibility (Durant, 2003), or (ii) using cultivars with a lower cell wall content. However, whether these measures could improve digestibility sufficiently is unclear as avian digestion of different grass species and cultivars has not been well-studied. Similarly, the gross energy content of improved pasture grass required to attract swans away from river feeding was impractically high; the gross energy content of vegetative plant tissues is unlikely to exceed 25 kJ g^{-1} DM (van Gils *et al*., 2008; Koukolova *et al*., 2010; **Chapter 7**). Even increased inputs of fertiliser would be unlikely to achieve the required energy content, and such inputs would also increase management costs and may be inappropriate in some chalk river catchments which are of high conservation values (Environment Agency, 2004). Pasture grass yields a relatively low rate of energy gain to swans due to the low intake rate and digestibility (**Chapter 7**), which limits the effectiveness of pasture grass as a sacrificial crop. Increasing pasture grass biomass would increase the intake rate available to the swans, although the low rate of intake rate increase with food biomass means that the benefit would be small for a given increase in biomass (**Chapter 7**; **Figure 7.4**). Alternative sacrificial crops, which offer a higher rate of energy gain, may be more effective at alleviating the grazing conflict. For example, oilseed rape has been previously been successfully used as a sacrificial crop for swans (Spray *et al*., 2002). Winter wheat (*Triticum spp*.) and barley (*Hordeum spp*.) are also popular food resources for flocks of swans (Laubek, 1995; Crawley Jr & Bolen, 2002). Alternatively, clover (*Trifolium spp*.) is a popular livestock forage crop and thus may have nutritive characteristics which make it more suited to use as a sacrificial crop (Koukolova *et al*., 2010). However, there is currently a lack of data on swan foraging on terrestrial plants other than pasture grass; in particular the functional response and digestibility are not known for either oilseed rape, wheat or clover. This lack of data prevented the evaluation of these plants in this study. Further experimental measurements of swan foraging capabilities on different plant species will aid in the design and evaluation of effective sacrificial feeding areas.

Increased water velocity, for example through a narrowing of the river channel, was shown to be a more promising option to alleviate the swan grazing conflict. Whilst narrowing the channel could result in a reduced area for plants to grow in, water crowfoot growth and abundance would not only benefit from the lack of grazing at higher water velocities, but also from the increased photosynthetic rates that occur due to the higher

rate of carbon and oxygen transfer between water and leaves that occurs at higher water velocities (Westlake, 1967). Swans were forced to switch from river to pasture at water velocities of 0.87 m s^{-1} or above; which is within the seasonal range of flow speeds reported for chalk rivers, albeit at the upper end of the range (Dawson & Robinson, 1984; Armitage & Cannan, 2000; **Figure 8.5**). A more practical option, which requires a change in flow speed over a smaller area and of a lower magnitude, may be to use localised increases in water flow speed to exclude swans from an area of river of high conservation or amenity value, *i.e.* a river-river switch. Swans were predicted to leave the model river patch as soon as flow was increased above that outside the model. Conversely, water crowfoot depletion was greater when flow speed within the model was lower than in the outside area. However, depletion did not vary with velocity in a linear way; at the lowest tested flow speeds depletion was reduced, probably as the birds could achieve a higher net energy gain and thus consumed less water crowfoot to meet their energy requirements.

However, there are three practical challenges to the successful use of increased water velocity as a management tool, either to facilitate a river-pasture or river-river shift, to alleviate swan grazing. Firstly, increasing water velocity in chalk rivers, many of which already suffer from low flows, may not always be desirable or practical (Environment Agency, 2004). However, in many chalk rivers localised restoration measures are already being undertaken to increase water velocity over short river reaches to alleviate other environmental problems such as sedimentation of river gravels (Environment Agency, 2004). Such measures should therefore be possible within the wider management objectives for chalk rivers. Secondly, water crowfoot stands retard the passage of water and thus create deeper but slower-flowing river reaches (Marshall & Westlake, 1990). In this way water crowfoot creates the optimal conditions for swan grazing. The problem here is that early increases in water velocity and the facilitated higher water crowfoot biomass could be offset by later decreases in water velocity which could attract swans back onto the river reach. Thirdly, there may be a risk that increasing flow speeds may run off large volumes of water and thus lead to less water (and thus a lower flow) later in the year. In addressing these challenges it is helpful to consider the life history of mute swans. Each summer, between mid-June and mid-August, non-breeding mute swans moult their flight feathers and are thus flightless during this period (Birkhead & Perrins, 1986; **Chapter 5**). Therefore these swans tend to remain in the same location throughout this period. This annual event could be used to inform the management objectives with regard to swan grazing conflicts. For example, early management action which increased flow speed in, and thus excluded swans from, a river reach would only need to maintain these elevated flows until mid-June, after which the swans would be flightless and thus would be unlikely to move. Whilst swans could graze this reach after mid-August (*i.e.* after the moult period) this would still have achieved a substantially reduced grazing

season of mid-August to October, rather than the normal April-May to October (**Chapter 5**; **Figure 5.5**). In addition, swans are known to favour large, open sites as moulting areas, thus narrowing the river channel as part of a flow modification plan would likely make that site less attractive to swans around the moult period (Birkhead & Perrins, 1986; **Chapter 5**).

The model assumed that swans had a perfect knowledge of the net rates of energy gain available within each patch and in the surrounding area (*i.e.* outside of the model area); this assumption appears valid given that swans are large highly-mobile foragers, known to move both within and between river catchments (Birkhead & Perrins, 1986; **Chapter 5**). O'Hare *et al*. (2007) showed that where grazing by flocks of swans occur, the growth rate of water crowfoot is reduced to 0 g d^{-1}, therefore I used this value in the model. However, in the scenarios where swans switched from river to pasture, water crowfoot growth rate would likely have been higher. Similarly, if cattle grazing was not permitted in the improved pasture grass field, grass growth rate would probably have exceeded 0 g d^{-1}; however, this was unlikely to have affected my conclusions as grass biomass depletion due to swan herbivory was relatively small. Thus the model probably underestimated the benefits to water crowfoot biomass of preventing grazing. Whilst the IBM used in this study, MORPH (Stillman, 2008), does allow the incorporation of parameter variance, I lacked the required estimates of the error associated with key parameters, such as pasture grass intake rate and food resource digestibility. As such the model presented here was deterministic (*sensu* **Chapter 6**) and so did not allow me to estimate the uncertainty associated with the model predictions. However, the sensitivity analysis indicated that predictions of depletion would vary with water crowfoot biomass. The sensitivity of the model to the initial biomasses of water crowfoot, both within and outside model patches, was unsurprising given that such values strongly influence food availability and intake rate. However, predictions of depletion were affected < 5 % by variance in all other parameters. In particular, the relative insensitivity of the predictions of depletion to the value of water crowfoot digestibility was reassuring as my value was assumed to be the same as mute swan digestibility of eelgrass *Zostera marina* L., another species of submerged macrophyte.

The approach used in this study demonstrated how proposed solutions to wildlife conflicts can be evaluated using an individual-based model, which can accurately predict the carrying capacity, food resource depletion, relative habitat use, and foraging times. Both the options identified in this study could be designed to yield multiple benefits to the ecosystem beyond just alleviating swan grazing, and as such represents an important improvement on traditional single-issue management.

Chapter 9: Swan-plant interactions in a chalk-river catchment: conclusions.

9.1 Introduction

Ecology has sometimes been criticised for its division between those who see ecology as a rigorous science in the pursuit of knowledge, and those who see ecology as a basis for solving environmental problems (Belovsky *et al*., 2004). I would argue that robust science facilitates good environmental management and that the complexity of many environmental problems provide ideal opportunities to test and refine our ideas of how ecological systems work. In this thesis I have attempted to show how ecology can be used as both a science and a tool; I have addressed fundamental scientific questions about how organisms interact, how populations are regulated, and what determines the distributions and behaviours of organisms, whilst examining the applied issue of how a grazing conflict can be quantified and managed.

9.2 Quantifying swan-plant interactions

The majority of the studies available to the waterfowl impacts meta-analysis in **Chapter 2** were conducted in shallow lakes (18 of 26). In contrast only a single study had examined shallow rivers (O'Hare *et al*., 2007). Given the large numbers of waterfowl which use rivers, and the ecological importance of birds within river ecosystems, greater future study of waterfowl-plant interactions in rivers is needed (Mason & Macdonald, 2000; Hoyer *et al*., 2006). The current study of herbivory appears biased towards a narrow range of habitats, such as lakes, and a narrow range of taxa, such as geese; as such, our current understanding of waterfowl herbivory is probably not representative of the range of interactions found in nature.

The methods of quantifying plant abundance used in this thesis each had considerable error associated with them, as I tried to optimise accuracy and sampling effort. Whilst the mere fact that such errors have been quantified was an advance on many previous studies, such errors doubtless affected my ability to detect spatiotemporal patterns in plant abundance as well as plant responses to herbivory and other factors. Further development of quick, efficient sampling techniques, which increase the number of samples which can be taken per unit time, is needed to allow greater accuracy in the quantification of plant-herbivore interactions.

9.3 The chalk river grazing conflict

Previous research has yielded some evidence that mute swans reduce the biomass of both terrestrial and aquatic plants in chalk river catchments (Harrison, 1985; O'Hare *et al*., 2007; Porteus *et al*., 2008). However, the wider effects on the aquatic plant community were unknown. How swan effects varied in space (*i.e.* between different sites within a river catchment) and time (*i.e.* between phases of the plant growth cycle) were also unknown. In **Chapter 4** I focussed on the aquatic plant community as this is of greater conservation and social importance due to the diverse wildlife assemblage and sport fisheries that it supports (Ladle & Westlake, 1976). Previous studies of waterfowl herbivory have typically ignored the seasonal cycles of growth and recession that occur in temperate ecosystems; studies instead often focus solely on grazing effects in a single point in the growth cycle (*e.g.* O'Hare *et al*., 2007; Gayet *et al*., 2011b). Given the wealth of factors which can influence plant growth and reproduction (Bornette & Puijalon, 2011), it is perhaps surprising that many studies consider the effects of waterfowl herbivory in isolation, without attempting to quantifying the effects of other such factors on the plant community (*e.g.* Esler, 1989; Conover & Kania, 1994; Bortolus *et al*., 1998; O'Hare *et al*., 2007; Tatu *et al*., 2007; Hartke *et al*., 2009). My results indicate that when these other factors are considered, a more detailed understanding of the effects of herbivory can be achieved. The results in **Chapter 4**, taken with previous research, indicates that a grazing conflict occurs where flocks of swans congregate at high densities in river reaches. Whilst I undertook my research within a single river catchment, my results will be applicable to other chalk rivers, and shallow lowland rivers in general, as the River Frome is typical of such rivers in terms of land use, hydrology, ecological community and nutrient concentrations (Environment Agency, 2004).

Given the ecological importance of aquatic plants, in particular water crowfoot, in the chalk river ecosystem, the effects of swan grazing on the plant community are likely to have wider effects. It has already been demonstrated that swan flock grazing of aquatic plants can lead to lower river depths, as plant material in the water column physically retards the passage of water (Wessex Water, 2008). Given that low water levels in chalk rivers are already a major concern to river managers due to climate change and abstraction, mitigation measures may also need to consider the effects of swans (Environment Agency, 2004). The potential effects of swan herbivory on macroinvertebrates and fish are of particular concern, due to their importance to conservation and sport fishing (Environment Agency, 2004). Whilst no studies to date have examined whether swan-plant interactions may affect other organisms in shallow rivers, there is some evidence of the consequences of plant loss due to other methods of

removal such as mechanical cutting, herbicide application, and shading by riparian vegetation or artificial materials (Dawson, 1978; Armitage *et al*., 1994; Roussel *et al*., 1998; Riley *et al*., 2009). Previous research has shown that lower invertebrate abundances are typically found in plant stands due to lower habitat availability (Wright *et al*., 1983; Wright, 1992; Tod & Schmid-Araya, 2009). Wright *et al*. (1983) reported that macroinvertebrate diversity and abundance differed between stands of plants of different species. Thus the effects of swan herbivory on plant species evenness (**Chapter 4**) may alter macroinvertebrate community structure relative to ungrazed areas. However, the effects of localised, short-duration reductions in plant abundance on river invertebrates are unclear. Whilst Armitage *et al*. (1994) found no effects of plant removal on invertebrates, Kaenel *et al*. (1998) reported a 65 % reduction in total number of invertebrates following a 85 % reduction in plant biomass. Similarly, fewer fish are typically found in reaches with lower plant abundance due to lower food (*i.e.* invertebrates) availability and cover from flow and predators (Roussel *et al*., 1998; Riley *et al*., 2009). Riley *et al*. (2009) reported lower invertebrate production and diversity, as well as reduced Atlantic salmon and brown trout densities and individual body size at sites with high proportions of riparian shading and little in-stream aquatic plant cover compared with less shaded sites with greater in-stream plant cover. In a plant removal experiment Roussel *et al*. (1998) found higher total fish densities in the vegetated reaches (~160 ind. 100 m^{-2}) relative to the de-vegetated reaches (~95 ind. 100 m^{-2}). However, different species showed different numerical responses to plant removal; densities of European minnow (*Phoxinus phoxinus* L.), European eel (*Anguilla anguilla* L.), gudgeon (*Gobio gobio* L.) bullhead (*Cottus gobio* L.) and stone loach (*Barbatula barbatula* L.) were higher in vegetated reaches, whilst 0+ Atlantic salmon densities were twice as high in the de-vegetated reaches. However, another study found that salmon exhibited a preference for moderately-vegetated (26-50 % cover) reaches over unvegetated or heavily-vegetated reaches (Beland *et al*. 2004). The mortality of 0+ brown trout was also found to be greater in reaches where aquatic plants had been cut (Mortensen, 1977). Swans reduce plant abundance during the peak- and recession-phases (May to September), which is when invertebrates and fish have the greatest need for cover as water levels are at their seasonal minimum (Hearne & Armitage, 1993; Armitage & Cannan, 2000). Thus the reductions in plant abundance at high swan densities may reduce the abundances of both invertebrates and fish (**Figure 9.1**). However, detailed field studies of the numerical and behavioural responses of invertebrates and fish to losses of aquatic plants, particularly swan grazing losses, are required to quantify the wider effects of swan herbivory on the chalk river ecosystem.

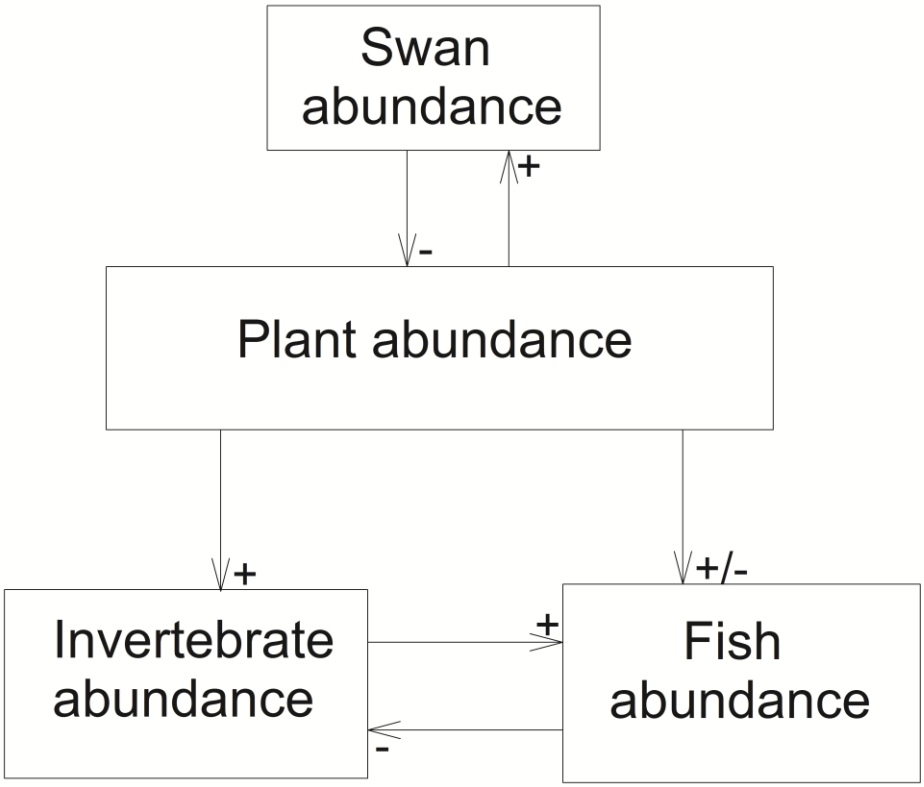


Figure 9.1: *A concept diagram illustrating the positive (+) and negative (-) relationships between the abundances of swans, aquatic plants, invertebrates and fish in the chalk river ecosystem.*

9.4 Managing grazing conflicts

The frequency and intensity of grazing conflicts are increasing in a number of herbivore-plant systems, for example ungulates in temperate woodlands, swans and beavers in shallow aquatic ecosystems, lagomorphs in grasslands, and waterfowl and ungulates in agricultural crops (Warren & Sutherland, 1992; Ankney, 1996; Nolet & Rosell, 1998; Côté *et al*., 2004; William *et al*., 2007; Dolman *et al*., 2010; **Chapter 2**; **Chapter 4**). Management of these grazing conflicts is complicated by the fact that the grazers are charismatic, which imposes additional ethical considerations and limits the options available to managers. By examining management options in the swan-chalk river grazing conflict, this thesis provides insight into how grazing conflicts between charismatic herbivores and valuable plants can be alleviated. Again, it should be stressed that in most instances the aim of management is not to prevent all herbivory, but alleviate the negative effects of herbivory. Indeed, herbivory is a desirable process in the maintenance of the diversity, structure, functioning and service provision of many

ecosystems (van Wieren & Bakker, 1998; Klaassen & Nolet, 2007; Hodder & Bullock, 2009; Taylor, 2009).

In terms of the management options I have examined in this thesis, habitat alterations are preferable to population control for two reasons; (i) habitat alterations are more ethical and likely to be acceptable to stakeholders as they require less, and crucially non-lethal, interference with the swan population; (ii) habitat alterations can be sustainable, as opposed to population control which needs to be repeated regularly at high intensities to be effective. Population control will always require further management as it does not address the fundamental reason why swans use aquatic plants in chalk rivers; swans elect to feed in the river when aquatic plants offer the highest available net energy gain (**Chapter 7**; **Chapter 8**). Habitat alterations that make a terrestrial food resource the most profitable, either by increasing the profitability of this terrestrial food resource (*e.g.* planting a sacrificial field of clover), or reducing the profitability of the aquatic plants (*e.g.* channel narrowing to increase water velocity), could offer a sustainable solution to grazing conflicts. Alternative currencies for behavioural decisions could also be explored; in this thesis I have focused on energy as (i) sufficient data on mute swan energetics were available, and (ii) energy has been shown to typically be a good proxy for fitness (Sih & Christensen, 2001). However, nitrogen could also be explored as many waterfowl are nitrogen-limited due to the relatively low protein content of plant tissues (Mattson, 1980). In particular, nitrogen could be important around the mid-June to mid-August moulting period, also a key period in plant management, as this is a period of relatively high protein demand for the birds (Birkhead & Perrins, 1986).

There are still many practical challenges to the successful implementation of habitat modification options, including the identification of key sites to protect, the willingness of riparian stakeholders to participate, and the suitability of alternative sacrificial crops. An additional benefit of habitat alterations is that they may deliver additional, multiple environmental benefits. For example, sowing a sacrificial field of clover, which produces abundant flowers, could aid threatened pollinator species such as bumblebees (*Bombus spp*.), whilst increased water velocity could prevent silt deposition (Environment Agency, 2004; Goulson *et al*., 2011; Stoate, 2011). Conversely, management actions taken to alleviate swan herbivory could have detrimental ecological or socioeconomic effects, and in such cases careful considerations of the relative costs and benefits must be made. Habitat alterations to alleviate swan grazing must be considered within the wider management of chalk rivers.

Habitat alterations are unlikely to be a suitable management strategy for every grazing conflict. For such measures to be effective, the herbivores must be both able and willing

to move between habitats. As such, habitat alterations may be effective for alleviating grazing conflicts with a range of herbivorous birds, mammals and winged invertebrates. However, other species may be unable or unwilling to move in response to changes in the relative profitability of different habitats. Animals that have limited movement (*e.g*. snails), face barriers to dispersal (*e.g.* fish), or are highly territorial (*e.g.* some ungulate species), may not move away from the plant species managers wish to protect from grazing. For example, grass carp (*Ctenopharyngodon idella* Val.) cannot move from one lake to another if they are not hydrologically connected, no matter how much more profitable the latter waterbody is. Other management options will need to be considered in such cases. Another potential disadvantage of habitat alteration is that, in order to evaluate whether is likely to be successful, it requires spatially- and temporally-explicit data on the herbivore dispersal ability, herbivore functional response, plant quantity and nutritional quality, and feeding costs for each habitat; such data may not be available for many herbivore-plant interactions. Furthermore, this point further illustrates how such fundamental biological data can be critical to effective management.

There are other possible management strategies which I have not explored in this thesis. In particular, the exploitation of the territoriality of breeding pairs could represent a useful tool if it could be harnessed. Breeding pairs of swans will attempt to exclude all other swans from the vicinity of their territory (Birkhead & Perrins, 1986), although non-breeders may still succeed in grazing within the territory if the territory is too large, the intruders too numerous, or the breeders too inexperienced, to defend (*e.g.* Parrott & McKay *et al*., 2001b). Parrott & McKay (2001b) used nesting platforms to encourage pairs to nest and thus defend the surrounding reaches, but the platforms were not used and grazing by flocks occurred. However, this may have been because the locations of the nesting platforms were based on habitat preferences of swans nesting along water courses in the English Midlands rather than chalk rivers; selection of nesting sites based on chalk river nest site preferences may achieve more success, but such data are currently lacking.

Crucially, this thesis has shown how robust science can underpin ecological management, and how challenging ecological problems can be used to further our understanding of complex biological systems. The approaches examined in this thesis were flexible, making few species- or ecosystem-specific assumptions, and as such could be used to address a wide range of plant-herbivore interactions. Given the increase in the frequency and magnitude of conflicts between herbivores and plants of ecological and socioeconomic importance, this thesis should provide useful insights into how such conflicts can be quantified and managed.

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Appendices

Appendix 1: Data for waterfowl impacts meta-analysis.

Information extracted from each study included in the meta-analysis of waterfowl impacts on plant standing crop. Between-site replicates refer to the number of different sites at which *R* was measured, for which a mean *R* value was derived. Between-year replicates refer to the number of different years in which *R* was measured, for which a mean *R* value was derived.

[1] species codes; a = mute swan *Cygnus olor*; b = Eurasian coot *Fulica atra*; c = black swan *Cygnus atratus*; d = black-necked swan *Cygnus melancoryphus*; e = northern mallard *Anas platyrhynchos*; f = gadwall *Anas strepera*; g = common teal *Anas crecca*; h = greylag goose *Anser anser*; i = tufted duck *Aythya Aythya*; j = common pochard *Aythya ferina*; k = common goldeneye *Bucephala clangula*; l = common shelduck *Tadorna tadorna*; m = northern shoveler *Anas clypeata*; n = Eurasian wigeon *Anas penelope*; o = red-crested pochard *Netta rufina*; p = common moorhen *Gallinula chloropus*; q = snow goose *Chen caerulescens*; r = Canada goose *Branta canadensis*; s = barnacle goose *Branta leucopsis*; t = coscoroba swan *Coscoroba coscoroba*; u = red-gartered coot *Fulica armillata*; v = white-winged coot *Fulica leucoptera*; w = yellow-billed pintail *Anas georgica*; x = red shoveler *Anas platalea*; y = yellow-billed teal *Anas flavirostris*; z = Chiloe wigeon *Anas sibilatrix*; ψ = silver teal *Anas versicolor*; .

[2] waterfowl densities given by Allison & Newton (1974).

Study	Species present[1]	Mean WID (ind. ha^{-1})	Mean WBD (kg ha^{-1})	Study length (days)	Study area (ha)	Between-site replicates	Between-year replicates	*R* (%)
O'Hare *et al*., 2007	a	7.2	0.7	22	18.0	1	1	49.2
Verhoeven, 1980	b	12.5	15.6	60	5.6	1	1	75.1
Sondergaard *et al*., 1996	b	5.2	6.5	60	21.0	1	1	61.0
Esler, 1989	b	5.5	6.8	75	1053.0	1	1	57.8
Perrow *et al*., 1997	b	2.7	3.4	118	5.5	1	1	23.2
Allin & Husband, 2003	a	17.5	1.7	90	84.6	3	5	55.1
van Donk & Otte, 1996	b	6.3	32.6	150	1.5	1	1	48.5
Corti & Schlatter, 2002	d	7.3	1.6	256	120.0	1	1	62.7
Sandsten *et al*., 2005	b,e,o,p	20.5	81.0	92	540.0	1	1	63.1
Hilt, 2006	a,b,e,i,j,k	1.1	1.1	91	730.0	1	1	42.9
Jupp & Spence, 1977[2]	b,e,f,g,i,j,k,l,m,n	0.6	1.8	200	1597.0	1	1	24.8
Lauridsen *et al*., 1993	b	16.0	20.0	60	15.0	4	1	62.4
Cargill & Jeffries, 1984	q	33.4	67.5	60	540.0	1	1	47.1
Esselink *et al*., 1997	h	7.2	2.1	210	1160.0	1	1	56.3
Haramis & Kearns, 2007	r	33.0	10.0	138	500.0	1	1	80.4
Masse *et al*., 2001	q	3.1	1.0	42	160000.0	1	2	32.5
Ydenberg & Prins, 1981	s	7.8	4.6	40	700.0	1	1	35.4
Smith, 2010	c	2.5	0.5	135	176.0	1	1	51.8
Dixon, 2009	c	5.2	1.0	60	600.0	3	1	57.0
Bortolus *et al*., 1998	d,t,u,v,w,x,y,z,ψ	2.3	1.5	31	82.0	1	1	16.7
Marklund *et al*., 2002	a,b,e,f,g,h,i,j,k	3.5	5.0	60	56.0	1	1	0.0
Lauridsen *et al*., 2003	b,e,j	1.5	1.5	69	44.0	1	1	40.7
Patton & Frame, 1981	h,s	20.3	3.6	85	2774.0	3	2	49.9
Rodriguez-Perez & Green, 2006	b,e,f,j,o	2.3	2.6	109	2997.0	1	1	29.0
Rodriguez-Villafane *et al*., 2007	b,e,f,n	14.8	42.0	59	4.5	1	1	36.7
Hidding *et al*., 2010	a,b,e,f,g	8.5	4.9	92	2100.0	1	4	59.6

Appendix 2: Data for waterfowl diet meta-analyses.

The table below lists the dietary information used in the analyses of the proportions of plant material consumed by waterfowl species (**Figures 2.4a** & **2.4b**). The symbol – indicates data not available.

Group	Species	Waterfowl mass (g)	Herbivory (% of total diet by dry mass)	Vegetative tissue consumption (% of plant material in diet)	Seed consumption (% of plant material in diet)	Reference
Dabbling Ducks	*Anas dicors*	397.3	13.8	-	-	Swanson & Bartonek, 1970
Dabbling Ducks	*Anas platyrhynchos* (♂)	1240.0	89.9	-	-	Combs & Fredrickson, 1996
Dabbling Ducks	*Anas platyrhynchos* (♀)	1080.0	91.7	-	-	Gruenhagen & Fredrickson, 1990
Dabbling Ducks	*Anas platyrhynchos*	1160.0	69.1	-	-	Dabbert & Martin, 2000
Dabbling Ducks	*Anas platyrhynchos*	1160.0	98.6	5.6	93.0	Allen, 1980
Dabbling Ducks	*Anas platyrhynchos*	1160.0	97.0	-	-	Delnicke & Reinecke, 1986
Dabbling Ducks	*Anas platyrhynchos*	1160.0	99.9	0.0	93.1	Miller *et al.*, 2009
Dabbling Ducks	*Anas platyrhynchos*	1160.0	94.4	0.0	100.0	Miller *et al.*, 2009
Dabbling Ducks	*Anas acuta*	951.0	99.9	0.0	98.4	Miller *et al.*, 2009
Dabbling Ducks	*Anas acuta*	951.0	99.2	0.0	100.0	Miller *et al.*, 2009
Dabbling Ducks	*Anas acuta*	951.0	49.5	-	-	Euliss et al., 1991
Dabbling Ducks	*Anas acuta*	951.0	84.9	21.8	78.2	Miller, 1987
Dabbling Ducks	*Anas erythrorhyncha*	567.5	94.1	-	-	Petrie, 1996
Dabbling Ducks	*Dendrocygna autumnalis*	827.5	98.6	-	-	Kramer & Euliss, 1986
Dabbling Ducks	*Dendrocygna autumnalis*	827.5	92.0	-	-	Bolen & Forsyth, 1967
Dabbling Ducks	*Dendrocygna autumnalis*	827.5	97.0	-	-	Bourne, 1981
Dabbling Ducks	*Dendrocygna*	827.5	97.0	-	-	Bruzual & Bruzual, 1983

	autumnalis					
Dabbling Ducks	*Anas clypeata*	606.5	50.0	53.3	39.1	Tietje & Teer, 1996
Dabbling Ducks	*Anas clypeata*	606.5	20.0	47.4	47.4	Tietje & Teer, 1996
Dabbling Ducks	*Anas clypeata*	606.5	7.5	-	-	Euliss *et al.*, 1991
Dabbling Ducks	*Dendrocygna bicolor*	744.7	97.7	1.8	97.8	Hohman *et al.*, 1996
Dabbling Ducks	*Dendrocygna viduata*	625.5	97.4	0.0	100.0	Petrie, 2005
Dabbling Ducks	*Dendrocygna arborea*	1024	100	-	-	Danforth, 1929
Dabbling Ducks	*Dendrocygna arborea*	1024	100	-	-	Staus, 1998
Dabbling Ducks	*Anas crecca*	754.5	99.9	-	-	Owen & Thomas, 1979
Dabbling Ducks	*Anas strepera*	744.4	99.1	82.6	0.02	McKnight & Hepp, 1998
Dabbling Ducks	*Aix sponsa*	675.5	97.1	3.7	93.4	Allen, 1980
Dabbling Ducks	*Aix sponsa*	675.5	95.0	-	-	Coulter, 1957
Dabbling Ducks	*Aix sponsa*	675.5	90.8	-	-	Coulter, 1955
Dabbling Ducks	*Cairina moschata*	2140.0	66.0	0.0	100.0	Woodward & Bolen, 1984
Dabbling Ducks	*Cairina moschata*	2141.0	100.0	-	-	Kear, 2005
Dabbling Ducks	*Amazonetta brasiliensis*	407.5	90.6	-	-	Madriz, 1983
Dabbling Ducks	*Anas rubripes*	1203.5	21.0	7.2	70.7	Reinecke & Owen, 1980
Dabbling Ducks	*Anas cyanoptera*	377.5	39.6	4.9	95.1	Gammonley, 1995
Diving Ducks	*Aythya ferina*	828.0	18.0	-	-	Sekiya *et al.*, 2000
Diving Ducks	*Aythya fuligula*	765.5	25.0	-	-	Sekiya *et al.*, 2000
Diving Ducks	*Oxyura jamaicensis*	579.5	9.8	-	-	Euliss *et al.*, 1991
Diving Ducks	*Oxyura jamaicensis*	579.5	38.2	-	-	Hoppe *et al.*, 1986
Diving Ducks	*Oxyura jamaicensis*	579.5	9.3	20.4	55.0	Woodin & Swanson, 1989
Diving Ducks	*Aythya valisineria* (♀)	1185.0	37.2	0.8	10.8	Noyes & Jarvis, 1985
Diving Ducks	*Aythya americana*	1021.5	62.4	74.3	21.3	Noyes & Jarvis, 1985
Diving Ducks	*Aythya americana*	1021.5	37.5	35.9	61.0	Woodin & Swanson, 1989
Diving Ducks	*Bucephala clangula*	981.8	65.0	-	-	Jones & Drobney, 1986
Diving Ducks	*Aythya marila*	1201.0	44.6	-	-	Badzinski & Petrie, 2006
Diving Ducks	*Aythya marila*	1201.0	22.3	-	-	Badzinski & Petrie, 2006
Diving Ducks	*Aythya marila*	1201.0	72.0	-	-	Jones & Drobney, 1986
Diving Ducks	*Aythya affinis*	814.0	71.5	0.0	100.0	Strand *et al.*, 2008
Diving Ducks	*Aythya affinis*	814.0	22.0	-	-	Badzinski & Petrie, 2006
Diving Ducks	*Aythya affinis*	814.0	13.7	-	-	Badzinski & Petrie, 2006
Diving Ducks	*Aythya affinis*	814.0	46.4	-	-	Badzinski & Petrie, 2006

Diving Ducks	*Aythya affinis*	814.0	81.0	-	-	Jones & Drobney, 1986
Diving Ducks	*Aythya affinis*	814.0	12.0	-	-	Hoppe *et al.*, 1986
Diving Ducks	*Aythya affinis*	814.0	23.0	0.0	100.0	Gammonley & Heitmeyer, 1990
Diving Ducks	*Aythya collaris*	709.0	44.0	19.3	56.8	Hohman, 1985
Diving Ducks	*Aythya collaris*	709.0	62.4	-	-	Hoppe *et al.*, 1986
Diving Ducks	*Bucephala albeola*	407.5	34.0	0.0	100.0	Gammonley & Heitmeyer, 1990
Geese	*Anser albifrons*	2315.0	100.0	91.1	0.0	Owen, 1976
Geese	*Anser albifrons*	2315.0	98.7	-	-	Budeau *et al.*, 1991
Geese	*Branta canadensis*	3300.0	100.0	59.3	15.4	Cadieux *et al.*, 2005
Geese	*Branta canadensis*	3300.0	100.0	-	-	Craven & Hunt, 1984
Geese	*Anser anser*	3481.5	100.0	19.8	0.0	Amat *et al.*, 1991
Geese	*Anser anser*	3481.5	97.9	71.0	25.0	Middleton & van der Valk, 1987
Geese	*Anser indicus*	2014.0	99.3	68.1	30.4	Middleton & van der Valk, 1987
Geese	*Chen caerulescens*	2500.0	91.7	79.7	0.0	Gloutney *et al.*, 2001
Geese	*Chen rossii*	1589.5	95.2	100.0	0.0	Gloutney *et al.*, 2001
Geese	*Anser erythropus*	2125.0	100.0	-	-	Markkola *et al.*, 2003
Geese	*Branta sandvicensis*	2047.5	99.0	-	-	Baldwin, 1947
Geese	*Branta sandvicensis*	2047.5	100.0	-	-	Black *et al.*, 1994
Geese	*Anser brachyrhynchus*	2500.0	100.0	-	-	Fox *et al.*, 2006
Swans	*Cygnus olor*	10350.0	99.0	89.4	1.8	Bailey *et al.*, 2008
Swans	*Cygnus melancoryphus*	4700.0	100.0	-	-	Corti & Schlatter, 2002
Swans	*Cygnus columbianus*	6750.0	98.7	-	-	Kear, 2005
Swans	*Cygnus columbianus*	6750.0	98.0	95.7	4.3	Earnst & Rothe, 2004
Swans	*Cygnus buccinator*	10785.0	99.9	-	-	Grant *et al.*, 1995
Swans	*Cygnus buccinator*	10785.0	100.0	76.1	2.0	Squires & Anderson, 1995
Swans	*Cygnus atratus*	5500.0	99.0	-	-	Kear, 2005
Rails	*Porphyrula martinica*	258.0	56.4	3.2	58.0	Tarano *et al.*, 1995
Rail	*Gallinula chloropus galeata*	270.0	55.0	1.1	69.5	Beltzer *et al.*, 1991
Rail	*Gallinula chloropus galeata*	270.0	55.0	1.0	97.0	Beltzer *et al.*, 1991
Rail	*Gallinula chloropus galeata*	270.0	55.0	0.7	98.6	Beltzer *et al.*, 1991
Rail	*Fulica americana*	900.0	97.0	-	-	Eichhorst,1989

Rail	*Fulica americana*	900.0	99.9	-	-	Stollberg, 1949
Rail	*Fulica atra*	800.0	84.1	-	-	Taylor, 1998
Rail	*Fulica atra*	800.0	63.5	-	-	Taylor, 1998
Rail	*Rallus elegans*	396.9	21.0	-	-	Meanley, 1956
Rail	*Rallus longirostris*	312.5	12.0	-	-	Taylor, 1998
Rail	*Porphyrio martinica*	218.3	71.0	-	-	Taylor, 1998
Rail	*Porphyrio marinica*	218.3	73.0	-	-	Taylor, 1998
Rail	*Porphyrio martinica*	218.3	58.0	-	-	Taylor, 1998
Rail	*Porphyrio porphyrio*	796.5	90.7	-	-	Taylor, 1998
Rail	*Fulica cristata*	737.0	97.4	-	-	Taylor, 1998
Rail	*Laterallus albigularis*	44.0	90.0	-	-	Taylor, 1998
Rail	*Coturnicops notatus*	30.0	80.0	-	-	Taylor, 1998
Sheldgeese	*Alopochen aegyptiacus*	2110.0	100.0	1.0	99.0	Halse, 1984
Sheldgeese	*Chloëphaga picta*	2930.0	100.0	-	-	Summers & Grieve, 1982
Sheldgeese	*Chloëphaga picta*	2930.0	100.0	80.3	13.9	Weller, 1975
Sheldgeese	*Chloëphaga rubidiceps*	1575.0	100.0	-	-	Summers & Grieve, 1982
Sheldgeese	*Plectropterus gambensis*	4439.0	98.0	-	-	Kear, 2005
Sheldgeese	*Tadorna radjah*	886.5	5.0	-	-	Kear, 2005

Appendix 3: Plant community General Linear Models.

The general linear models (GLMs) that explained the greatest percentages of between-site variance in each plant community metric. The relevant mean (± SE) parameter values for swan biomass density (SwanBD), shading (Shade), water temperature (Temp) and distance downstream of source (Dist), are given for each equation; n/a indicates that no statistically significant model was detected. *n* = 20 for each model.

Plant community metric	**Phase of plant growth cycle**	***F***	***P***	$R^2_{(adj)}$	**Equation**
Plant biomass	Growth	-	-	-	n/a
	Peak	8.89	0.008	28.3 %	= 713.00 ± (197.80) + (-8.56 (± 1.04) · Shade)
	Recession	5.92	0.011	34.1%	= 498.44 (± 94.91) + (-1.87 (± 0.59) · SwanBD) + (-9.47 (± 3.76) · Shade)
Plant cover	Growth	-	-	-	n/a
	Peak	44.58	< 0.001	91.6 %	= (-11.32 (± 4.41) · SwanBD) + (1.84 (± 2.73) · Temp) + (6.97 (± 2.14) · Dist) + (0.78 (± 0.31) · (SwanBD · Temp)) + (-0.46 (± 0.15) · (Temp · Dist))
	Recession	14.12	< 0.001	58.0 %	= 65.29 (± 10.61) + (-0.18 (0.04) · SwanBD) + (-1.01 (± 0.24) · Shade)
Water crowfoot flowering	-	5.74	0.028	20.0 %	= 47.27 (± 8.99) + (-0.21 (± 0.09) · SwanBD)

Water crowfoot dominance	Growth	-	-	-	n/a
	Peak	4.14	0.024	33.1 %	= 3526.86 (± 1262.91) + (-234.48 (± 87.65) · Temp) + (-31.23 (± 10.82) · Dist) + (2.12 (± 0.75) · (Temp · Dist))
	Recession	7.46	0.002	50.5 %	= 4694.43 (± 1350.60) + (-314.00 (± 93.36) · Temp) + (-42.61 (± 11.68) · Dist) + (2.89 (± 0.81) · (Temp · Dist))
Plant species richness	Growth	-	-	-	n/a
	Peak	5.35	0.010	40.7 %	= -220.61 (± 100.92) + (14.95 (± 7.00) · Temp) + (2.00 (± 0.87) · Dist) + (-0.13 (± 0.06) · (Temp · Dist))
	Recession	238.97	< 0.001	92.2 %	= 0.05 (± 0.01) · Dist
Plant species evenness	Growth	-	-	-	n/a
	Peak	6.00	0.025	20.8 %	= 0.30 (± 0.07) + (0.002 (± 0.001) · SwanBD)
	Recession	5.19	0.011	39.8 %	= -47.33 (± 13.83) + (3.27 (± 0.96) · Temp) + (0.43 (± 0.12) · Dist) + (-0.03 (± 0.01) · (Temp · Dist))

Appendix 4: Population model.

The program code below was used to run the stochastic swan population model in Python 3.1 (Python Software Foundation). The deterministic model was identical apart from SD = 0 for all parameters. This particular code is parameterised for the 'open' system with 0 % annual removal and no clutch manipulation (*i.e.* the 'no management' option).

```
# Swan population model

from random import gauss

from csv import writer


# Returns random number drawn from normal distribution

def normal(mean, sd, min, max):

    done = False

    while not done:

        value = gauss(mean, sd)

        if (min <= value <= max):

            done = True

    return value


# Returns number of breeding adults

def get_num_breed_ad():

    if (num_ad > (2 * num_terr)):

        return 2 * num_terr

    else:

        return num_ad
```

```
# Open result files and write header rows

raw_res = writer(open('raw_swan_res.csv', 'w', newline=''))

raw_res.writerow(['r', 'y', 'num_cyg', 'num_juv', 'num_ad', 'num_breed_ad', 'num_nonbreed_ad', 'num_swan', 'num_flock_swan'])

summ_res = writer(open('summ_swan_res.csv', 'w', newline=''))

summ_res.writerow(['y', 'mean_num_swan', 'l95_num_swan', 'u95_num_swan', 'mean_num_flock_swan', 'l95_num_flock_swan', 'u95_num_flock_swan'])


# Initialize constant parameters

num_rep = 1000 # Number of replicates

num_year = 51 # Number of years


# Initialize combined results

combined_num_swan = []

combined_num_flock_swan = []


# Loop through replicates

for r in range(num_rep):


    # Initialize starting population sizes

    init_num_cyg =     normal(58   , 9.19, 0, 100) # Initial number of cygnets

    init_num_juv =     normal(52   , 31.11, 0, 500) # Initial number of juveniles

    init_num_ad =      normal(147  , 2.83, 0, 500) # Initial number of adults


    # Initialize annual results

    annual_num_swan = []
```

```
annual_num_flock_swan = []


# Loop through years

for y in range(num_year):


    # Initialize year-dependent parameters

    cyg_surv =          normal(0.37 , 0.36, 0,    1) # Cygnet survival per year

    juv_surv =          normal(0.73 , 0.25, 0,    1) # Juvenile survival per year

    nonbreed_ad_surv = normal(0.71 , 0.23, 0,     1) # Non-breeding adult survival per year

    breed_ad_surv =    normal(0.9  , 0.11, 0,    1) # Breeding adult survival per year

    num_terr =          normal(38   , 9.24, 0, 100) # Number of territories

    cyg_per_breed_ad = normal(2.2 , 2.80, 0, 10) # Number of cygnets per breeding adult

    cyg_immig =         normal(0    , 0, 0, 1) # Number of cygnets immigrating per year

    juv_immig =         normal(6.9    , 2.74, 0, 100) # Number of juveniles immigrating per year

    ad_immig =          normal(43.2   , 17.81, 0, 500) # Number of adults immigrating per year

    AR =                normal (0.0 , 0, 0.0, 0.0) # Annual Removal of non-breeding birds


    # Calculate results during first year

    if (y == 0):

        num_ad = init_num_ad

        num_breed_ad = get_num_breed_ad()

        num_nonbreed_ad = num_ad - num_breed_ad

        num_juv = init_num_juv
```

```
            num_cyg = init_num_cyg


        # Calculate results during later years
        else:
            num_ad = ((num_juv + num_nonbreed_ad + ad_immig) * nonbreed_ad_surv)+
(breed_ad_surv * num_breed_ad)
            num_breed_ad = get_num_breed_ad()
            num_nonbreed_ad = (num_ad - num_breed_ad) * (1 - AR)
            num_juv = (((juv_surv * num_cyg) + juv_immig)) * (1 - AR)
            num_cyg = ((cyg_per_breed_ad * num_breed_ad) * cyg_surv) + cyg_immig


        # Find total number of swans and number of flock swans
        num_swan = num_ad + num_juv + num_cyg
        num_flock_swan = num_nonbreed_ad + num_juv


        # Update annual results
        annual_num_swan.append(num_swan)
        annual_num_flock_swan.append(num_flock_swan)


        #  Save raw results
        raw_res.writerow([r, y, num_cyg, num_juv, num_ad, num_breed_ad,
num_nonbreed_ad, num_swan, num_flock_swan])


    # Update combined results
    combined_num_swan.append(annual_num_swan)
    combined_num_flock_swan.append(annual_num_flock_swan)
```

```
# Calculate summary statistics
mean_num_swan = []
l95_num_swan = []
u95_num_swan = []
mean_num_flock_swan = []
l95_num_flock_swan = []
u95_num_flock_swan = []
for y in range(num_year):
    sum_num_swan = 0
    sum_num_flock_swan = 0
    sort_num_swan = []
    sort_num_flock_swan = []
    for r in range(num_rep):
        sum_num_swan += combined_num_swan[r] [y]
        sum_num_flock_swan += combined_num_flock_swan[r] [y]
        sort_num_swan.append(combined_num_swan[r] [y])
        sort_num_flock_swan.append(combined_num_flock_swan[r] [y])
    mean_num_swan.append(sum_num_swan / num_rep)
    mean_num_flock_swan.append(sum_num_flock_swan / num_rep)
    sort_num_swan.sort()
    sort_num_flock_swan.sort()
    l95_num_swan.append(sort_num_swan[round(0.025 * (num_rep - 1))])
    u95_num_swan.append(sort_num_swan[round(0.975 * (num_rep - 1))])
    l95_num_flock_swan.append(sort_num_flock_swan[round(0.025 * (num_rep - 1))])
    u95_num_flock_swan.append(sort_num_flock_swan[round(0.975 * (num_rep - 1))])
```

```
# Save summary results

for y in range(num_year):

    summ_res.writerow([y, mean_num_swan[y], l95_num_swan[y], u95_num_swan[y], mean_num_flock_swan[y], l95_num_flock_swan[y], u95_num_flock_swan[y]])



# Indicate that simulation has finished

print('Simulation finished')
```

Appendix 5: Determining pasture grass sample size.

To determine the sample size required to determine pasture grass biomass, in February 2010 I undertook intensive field sampling of 20 pasture fields around East Stoke (50°41'N, 02°11'W). At each site 50 samples were taken following the protocol for aquatic plants detailed in **Chapter 3** and **Chapter 4**. Bootstrap resampling with replacement was used to derive the relationships between sample size and accuracy of measuring mean pasture grass biomass. For each analysis, *n* samples were selected randomly from the datasets of abundance samples (g DM m^{-2}) and the mean was calculated. 10,000 iterations of this process generated a frequency distribution of mean biomass values derived from a sample size of *n*, from which the mean and 95 % confidence intervals were calculated, where R_{CI} was the range between the lower 5 and upper 95 percentiles of the Bootstrap frequency distribution. I calculated the percentage error of my biomass measurements by calculating R_{CI} as a percentage of the mean biomass for a given value of *n*; data from all sites were pooled to yield mean (± 95 % CI) values. Error decreased as sample size increased, but did not decrease below ± 18.6 % even where *n* = 50 (**Figure A5.1**). As the greatest decrease in error occurred as *n* increased from 1 to 5, I selected *n* = 5 for quantification of pasture grass biomass, as a compromise between accuracy and sampling effort.

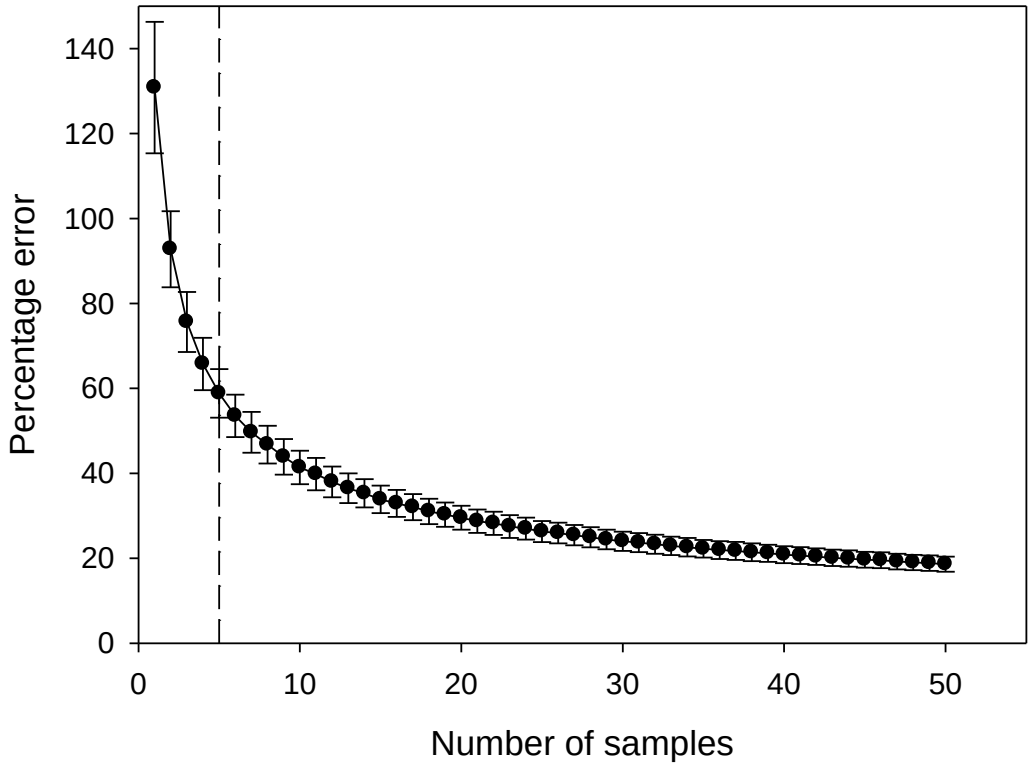

Figure A5.1: *The mean ± 95 % CI percentage error associated with estimates of mean pasture grass biomass (g DM m^{-2}) at a site for a given number of samples. The dashed line indicates the selected sample size of n = 5.*

Appendix 6: Swan time budgets.

To assess the accuracy of the individual-based model predictions (**Chapter 8**), I collected field data on the time swans devote to foraging during the time of year simulated by the model.

The River Frome catchment at East Stoke was surveyed for swan flocks between 18th-28th May 2009. Where flocks of swans were encountered, a minimum of four flock birds were filmed simultaneously using a tripod-mounted Canon Legria HFS10 HD video camera (Canon Inc., Japan) for 15 ± 2 minutes. Filming was conducted between dawn and dusk as mute swans are generally diurnally active and rest during darkness (Jozkowicz & Gorska-Klek, 1996; Meissner & Ciopcińska, 2007). Analyses of swan behaviours was performed using 'Event', a purpose-built event recorder which permits frame by frame viewing, which has been used in previous studies to quantify recorded behaviours (Baker *et al.*, 2010). For each video all individuals within the video frame were watched separately, recording the number and duration of bouts of all foraging behaviour over a contiguous 10 minute period, after O'Hare *et al*. (2007).

Seven flocks, comprising 64 individuals, were filmed. The mean (± 95 % CI) percentage time devoted to foraging was 31.9 ± 11.9 %. Whilst I cannot exclude the possibility that the same individual was filmed twice, the fact that no ringed individuals were filmed twice makes this unlikely.